A BIOPHYSICAL STUDY OF CONNECTIVITY IN EARLY LIFE HISTORY STAGES OF COASTAL NEWFOUNDLAND FISHES

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A Biophysical Study of Connectivity in Early Life History Stages of Coastal Newfoundland Fishes

By

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Abstract

This study addresses the biophysical factors that influence population connectivity during the early life history of Atlantic cod (*Gadus morhua*) in coastal Newfoundland. In Chapter 1, I review how connectivity is regulated by biophysical processes and should be a central consideration in spatially-oriented management and conservation. The second chapter illustrates connectivity associated with a known source of pelagic eggs (Smith Sound). Dispersal patterns did not vary over the spring and summer period of egg production, with a net export estimated at 13%/day. Data suggests that connectivity is limited to Trinity Bay. The final chapter addresses larval behavioural contributions to connectivity. Concomitant increase in spatial heterogeneity with the transition to an inertial swimming environment and spatial association with upstream optimal nursery habitats suggest that swimming influences dispersal and connectivity. This study demonstrates how a better understanding of connectivity is better achieved through synergistic study of biophysical interactions.

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Statement of co-authorship

The author of this thesis designed field sampling protocols, participated in the collection and processing of all data, analyzed and wrote all the subsequent manuscripts. Dr. Paul Snelgrove and Dr. Brad deYoung made substantial contributions to field sampling design and the evolution of data interpretation, and also provided editorial reviews of all the chapters. Co-authors for future publications resulting from these chapters have not been determined but will likely include committee members Dr. Paul Snelgrove, Dr. Brad deYoung, and Dr. Robert Gregory.

Introduction and Overview

Marine fisheries literature of the Twentieth First Century has increasingly focused on conservation, sustainability, and potential productivity. Globally, fisheries resources account for ~ 20% of world animal protein consumption and provide primary employment to over 200 million people globally (Botsford et al. 1997). Despite their value, many ocean fisheries resources are in peril. Globally fisheries are yielding progressively lower catches, despite constant or increasing fishing effort (Watson and Pauly 2001). Commercial fishing can reduce community biomass by approximately 80% within 15 years of exploitation. It is estimated only 10% of the pre-industrial large predatory fish stocks currently remain, the decline of which is largely due to fishing activities (Myers and Worm 2003). Disturbing results like these have spurred new research that focus on determining the primary factors that maintain marine population structure and how these factors can help to conserve natural populations.

In order to apply conservation strategies effectively, it is important to understand what factors influence the spatial dynamics of the population of interest (Panteleev et al. 2004; Bradbury et al. 2008; Snelgrove et al. 2008). Connectivity defines the degree of exchange of individuals between two discrete sources, which is mediated by dispersal during the early life history (i.e., egg and larvae stages of an organism; (hereon in ELH) (Cowen et al. 2007). Understanding the linkages and spatial dynamics of populations during all ontogenetic stages of an organism is essential to understanding connectivity. Connectivity influences not only spatial structure but the large-scale temporal stability of a population (Hastings and Botsford 2006). During ELH, connectivity is strongly driven by the

physical environment (Bradbury et al. 2003). The physical environment influences egg stage development (Pepin et al. 1997), dispersal potential (deYoung and Rose 1993), both egg (Parada et al. 2003) and larval bouyancy (Saborido-Rey et al. 2003), larval growth (Guan et al. 2008; Bodchadsky et al. 2008)), and the swimming environment around the developing larvae (Fuiman 1997). Biological-physical interactions drive the successful transport of early life stages in critical habitat (Cushing 1990; deYoung and Rose 1993; Snelgrove et al. 2008). For the population as a whole, the successful transition from the early life history stages to the juvenile stage (recruitment) is vitally important (Smedbol et al. 1998). Despite the overwhelming evidence that dispersal is a key factor in defining population structure, published estimates of dispersal in the marine realm are few (Levin 2006).

My thesis addresses spatial structure and connectivity in a single bay, within the context of the physical environment. My first chapter provides a comprehensive literature review of the linkages between the physical environment, dispersal, and connectivity, with a particular focus on fish species. It also highlights key biological-physical interactions and, in so doing, lays the groundwork for the next two chapters. My second chapter illustrates the temporal and spatial patterns of eggs and larvae within a source region and radiating out from it. Various models, created in Matlab and used in conjunction with field data, provide a basis for estimates of dispersal and connectivity from Smith Sound in Trinity Bay, NL. The establishment of spatial pattern through ontological development during ELH are then examined from the Smith Sound point source. This model framework is then used in analyses to determine what factors influence connective or dispersive

patterns from cod originating in Smith Sound. Temporal variation is addressed both seasonally and annually, in a comprehensive examination of dispersal during the entire spawning period. The applicability of this model is then tested empirically using ichthyoplankton data obtained from four surveys within Trinity Bay. The final chapter addresses the degree to which active behaviour (e.g. swimming) influences connectivity. This topic is addressed by combining hydrodynamic theory, laboratory swimming experiments (data from Guan et al. 2008), and field observations. Again emphasis is placed on the overarching theme of how the physical environment provides the structure for the biological pattern.

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Chapter 1. Connectivity of the early life history stages of larval fishes: Evaluating the roles of the physical environment.

1.1 Introduction

"The deepest sin against the human mind is to believe in things without evidence"
Thomas Huxley.

For many aquatic species life is spent immersed in fluid, and not surprisingly the physical properties that characterize this fluid environment govern many of the biological processes we observe. In the marine realm, organisms have developed life history strategies that are tuned to this environment, enabling populations to disperse into favourable habitats and exchange individuals with other spatially extant populations. Dispersal is one of the most important life history traits in terms of its influence on evolutionary processes and population persistence (Mora and Sale 2002). For many marine organisms, dispersal occurs primarily in the planktonic environment during their early life history (egg and larval stages). Through circulation and current patterns, the pelagic environment provides a potential opportunity for extensive movement of propagules within and among populations (Cowen 2000). Survival in the pelagic zone is inherently variable as a result of the spatial patchiness of both predators (McGurk 1986) and food resources (Cushing 1990). Researchers have inferred that the pelagic dispersive stage provides a selective advantage through exchange of individuals among populations (Barlow 1981) while hedging against a pelagic environment that can be variable in its suitability for larval survival (Doherty et al. 1985).

For the most part, the pelagic dispersal phase is structured by the physical environment encountered by the organism during this dispersive stage (e.g., Baumann et al. 2003). Oceanographic currents, for example, have the potential to disperse passive eggs and early stage (i.e., limited motility) larvae over large distances (Cowen 2000; Bradbury and Snelgrove 2001). The duration of this pelagic dispersive stage is largely dependent on temperature which, in turn, dictates the extent of dispersal (Bradbury et al. 2003). Larval swimming ability has been acknowledged to be sufficiently strong to influence dispersal patterns in reef fish (Wolanski et al. 1997) and, more recently, in cold water fishes (Guan et al. 2008). The physical environment encountered by these small organisms can profoundly influence the potential contribution of swimming behaviour (von Herbing 2002). Because it influences almost all facets of dispersal, the physical environment provides a useful framework in which to examine connectivity, defined as the degree to which populations are reproductively linked.

The data gaps on marine population structure and function are particularly striking for early life history stages. The limited connectivity data available for early life history stages represents a significant obstacle to understanding population structure (Cowen et al. 2007) and successful implementation of marine management and conservation goals (Hastings and Botsford 2003). The following review summarizes research on marine connectivity and how it might be used as a tool in management of marine species.

My review also aims to demonstrate the influence of the physical environment in defining population structure through its effects on dispersion and connectivity of pelagic early life

history stages of marine fishes. The tandem assessment of physical and biological processes in early life history stages is necessary to evaluate connectivity and its role in structuring marine populations.

1.2 Modelling marine populations in a fragmented world

"The metapopulation concept is here to stay in marine ecology. Science demands it, fisheries management needs it, and it is the last hope for marine conservation."

Joan Roughgarden

The orientation of individuals, in both space and time, defines the structure within and among populations. One key issue in understanding how or what might influence the persistence of a species in a given environment is the evaluation of the population structure. Defining the most appropriate structure to apply to a marine system is often debated and is largely dependent on scale (Bradbury et al. 2000), which can differ significantly among populations and species. Maintaining the integrity of population structure is essential for the long-term persistence and sustainability of populations (Tilman and Downing 1994). A conceptual model that describes population structure and function can provide invaluable information about the factors that influence spatial persistence, and provide a defensible basis for many conservation and management decisions.

Research has demonstrated that marine ecosystems are comprised of a heterogeneous landscape of environmental conditions that determine key population parameters such as survival and persistence (Cowen et al. 2006). This heterogeneity, coupled with human activity (e.g., fishing disturbance), has fragmented critical habitat for many marine species and structured populations into a framework of discrete patches (Casagrandi and Gatto 2006). This concern is particularly relevant in light of evidence that fishing pressures can select against large-scale natural dispersal (Baskett et al. 2007), thereby promoting higher local retention. Recent genetic work has shown that populations of highly mobile and abundant species such as Atlantic cod (*Gadus morhua*), which were once thought to be relatively panmictic, actually exhibit substantial spatial structure (Ruzzante et al. 1996, 2000, 2001). In light of such findings, the concept of marine metapopulations has become increasingly accepted as a widely-applicable model to describe marine populations (Kritzer and Sale 2004). The metapopulation concept holds promise for use in conceptual models that provide a holistic understanding of what factors mediate population structure, and allow conservation biologists and fisheries managers to make more informed and robust decisions on threatened or commercially-valuable species (Hutchings 1996; Smedbol and Wroblewski 2002).

Defining marine metapopulations

Historically, a metapopulation was described as a "population of populations", consisting of discrete population units with some degree of exchange of individuals, or connectivity, and probability of extinction (Levins 1969). Levins (1969) work was originally applied to terrestrial insect populations, but the utility of this model for describing fragmented

populations has led to its use in the marine realm (Smedbol and Wroblewski 2002; Kritzer and Sale 2006). These studies have frequently applied the metapopulation concept in the absence of empirical data (Grimm et al. 2003), while others have done so without clearly defining what is meant by metapopulation (e.g., Smedbol and Wroblewski 2002). Two schools of thought surround the application of Levins (1969) conceptual model to marine systems and these schools are divided on whether to incorporate differences in extinction probability when defining spatial heterogeneity (Kritzer and Sale 2004). Smedbol and Wrobleski (2002) and Grimm et al. (2003) argue that a marine metapopulation is comprised of a set of semi-independent populations of which at least one must have some probability of extinction as that metapopulation persists. The focus on extinction probability links to the observation that environmental conditions must vary among sub-population units so that they are truly independent in the absence of any connective processes (Grimm et al. 2003). Other authors use a more simplistic view in which a metapopulation is defined as a set of semi-independent breeding units with limited exchange of individuals (Hanski and Gaggiotti 2004; Kritzer and Sale 2004, 2006). The more relaxed definition emphasizes the importance of metapopulation structure in defining linkages between local- and regional-scale processes (Kritzer and Sale 2004), and offers a method to study and analyze a wider variety of fragmented marine populations.

When the original tenets of Levins' model are relaxed and the focus is placed on defining linkages, it is possible to model a wide variety of possible spatial population structures within a metapopulation framework (Kritzer and Sale 2004). For example, mixed

metapopulations illustrate a situation where a few subpopulations are very closely linked and provide dispersers to more isolated subpopulations (e.g., Atlantic cod, Smedbol and Wroblewski 2002). Source-sink models refer to a system consisting of subpopulations with positive growth (sources), which provide individuals to subpopulations with negative growth (sinks) (Crowder et al. 2000). Mainland-island models describe populations where one large, temporally-persistent subpopulation (the mainland) provides individuals to much smaller and less persistent satellite subpopulations (islands) (Freckleton and Watkinson 2002). These frameworks demonstrate the flexibility of metapopulation models and exemplify how connectivity fundamentally underpins their use. Once applied, these models can highlight processes that are vital to spatial persistence, therefore directing marine management and conservation initiatives (Gaines et al. 2007).

Conservation and marine metapopulations

Marine conservation initiatives typically focus on maintaining a particular species or feature (e.g., habitat) through the removal of human pressures such as fishing (Murray et al. 1999; Botsford et al. 2001). These areas are often referred to as marine reserves or marine protected areas (Cowen et al. 2007), and in the absence of fishing pressure may become sanctuaries where populations can increase in abundances to a level where they can self-seed and also seed adjacent unprotected areas (spillover), thereby offsetting the cost of lost access. This design offers fishery managers some insurance against overexploitation (Murray et al. 1999) that is relatively cheap to implement (Halpern 2003). This conservation tool can be utilized singularly or within a network. Marine

reserve networks not only supplement mean population levels but can also conserve some aspects of spatially-distributed metapopulations, so that the sum effect is greater than the parts. The shift in embracing biological spatial data into the design of marine reserve networks meshes conservation goals with spatially-oriented management that utilizes metapopulation models to describe marine populations (Hastings and Botsford 2003).

Successful design and implementation of marine reserves or networks often hinges on knowledge of connectivity and dispersal. Connectivity considerations can influence decisions on the size of a reserve. Large reserves may not export sufficient propagules to suitable non-managed areas. In contrast, small reserves might not self-recruit, potentially leading to local extinction within the reserve (Botsford et al. 2001; Alpine and Hobday 2007). Metapopulation models highlight the critical linkages that underlay population structure and provide the baseline data needed for successful marine reserve network design (Gaines et al. 2007). Connectivity can mediate survival in adjacent areas (termed the 'rescue effect', Brown and Kodric-Brown 1997), and can maintain population structure in the presence of local extinctions. In addition to size, appropriate spacing is needed to ensure that propagules can disperse between and within the spatial network. Lack of empirical data on dispersal processes can also lead to ineffective placement of marine reserves, often leading to reduced recruitment or population levels (Fogarty 2000). Baskett et al. (2007) suggest that marine reserves that are too large might select for short dispersal, because survival probability often decreases outside the reserve (e.g., Halpern 2003) declining the utility of a single large reserve, versus a network of smaller reserves,

design. Clearly, connectivity must be considered as a guiding factor in the design of marine reserves and networks.

Crucial gaps in understanding marine metapopulations

Despite a clear need for better ocean management, there is little empirical data on connectivity to use in design of effective marine reserves (Botsford et al. 2003; Cowen et al. 2006; Fogarty and Botsford 2007). Many marine reserves have been designed and implemented based on political or societal pressures rather than relevant biological data (Sala et al. 2002; Grimm et al. 2003; Halpern 2003). Several reviews have summarized strong evidence that marine reserves can meet the goals of increasing mean population levels in and outside management boundaries (Hastings and Botsford 2003; Halpern 2003; Palumbi 2004), however, designs that do not incorporate an understanding of connectivity may never attain management and conservation objectives. Despite the theoretical appeal of metapopulation models, a lack of quantitative information on connectivity during early life histories generates uncertainty about their efficacy for marine management and conservation goals (Fogarty and Botsford 2007).

1.3 The role of biological-physical linkages in defining connectivity

"Fluid is the skeleton fleshed out in biological design"
Steven Vogel

The scale and extent of connectivity in linking populations is dependent on the exchange of individuals which, for many marine organisms, is primarily accomplished through pelagic dispersal during their early life history (Cowen et al. 2007). Dispersal is

inherently a product of biological-physical processes that regulate species responses at large and small scales (Gawarkiewicz et al. 2007). These processes, driven by either passive drift or active swimming, fall within the bounds of the mechanical constraints of the fluid environment in which they occur. In this sense the physical environment is the driving mechanism for the dispersive processes that influence large-scale population characteristics (Mann and Lazier 2006). Many authors have examined the role of the physical environment in dispersal and recruitment of organisms with pelagic dispersal stages. Research on temperature and egg development (Bradbury et al. 2001), egg survival (Pepin 1991), oceanographic forcing (deYoung and Rose 1993, Van der veer et al. 1998), upwelling (Ings et al. 1997), larval swimming (von Herbing 2002; Guan et al. 2008), salinity (Nissling and Westin 1991), and even buoyancy of eggs (Parada et al. 2003) and larvae (Saborido-Rey et al. 2003) have been implicated in recruitment variability. The relationship between the physical environment and production has been shown to differ among species with different spawning strategies, with a suggested 'tuning' of spawning to optimal developmental environments (Snelgrove et al. 2008). A better understanding of spatial and temporal variability in dispersal during the early life history is essential to effective implementation of conservation strategies such as marine reserves (James et al. 2002; Palumbi 2004; Apline and Hobday 2007), metapopulation models (Kritzer and Sale 2006), and our understanding of key influences on local population dynamics (Gaines et al. 2007).

Biological-physical interactions and passive dispersal

Passive dispersal predominates in egg and early larval development stages where there is little or no behavioural contribution to spatial patterns (Hjort 1914). Thus, pelagic life history stages are often considered to be passive particles whose spatial pattern is dictated primarily by local circulation features. The movement and development of these particles is crucial to understanding how connectivity and large-scale processes regulate population dynamics. The importance of this passive dispersive stage was highlighted by Harden-Jones (1968), who suggested the "migration triangle hypothesis" in which population spatial patterns are the product of circulation patterns that link spawning grounds to nursery habitats, thus regulating connectivity during the early life history.

The interplay between the physical environment and spawning biomass is fundamental to understanding recruitment variability in marine organisms (Harden-Jones 1968; Begg and Marteinsdottir 2002). Variables such as survivorship and recruitment are inherently linked to population stability (Bradbury et al. 2001) and spatial persistence (Botsford and Hastings 2006). Linkages between the physical environment and recruitment variability are numerous (e.g., Bradbury et al. 2003; Miller et al. 2006). Given the constraints imposed by the physical environment on dispersal (e.g., circulation and seasonal temperatures) timing of spawning in the context of circulation, development, and spawning strategy is vital in order to place eggs in a suitable environment for survival and recruitment (Snelgrove et al. 2008). Increased mortality rates are associated with a spatial/temporal mismatch with resources or suitable environments, leading to spawning propagules not reaching appropriate settlement sites (McCormick 1999), growing into or escaping prey fields of dominant local predators (Paradis et al. 1999), or prolonged

passive periods susceptible to heightened predation (Dahlberg 1979; Meekan and Fortier 1996). The timing and placement of spawning propagules into circulation patterns that facilitate retention or movement to optimal nursery areas has been formalized as the 'match-mismatch' hypothesis (Cushing 1990). Cushing (1990) suggested that overall abundance of fish larvae is regulated by concentration, where total larval abundance in a patch is limited by food resources. Bochdansky et al. (2008) provide an example of this relationship concluding that environmental conditions which increased predator-prey encounter rates were positively related to increased larval growth and survival of radiated shanny (*Ulvaria subbifurcata*). DeYoung and Rose (1993) suggested that tuning spawning to optimal physical variables as the 'right site' hypothesis. Specifically, they argued that Atlantic cod (*Gadus morhua*) spawn in areas where circulation patterns facilitate dispersal to optimal habitats or contribute to shorter pelagic durations. Iles and Sinclair (1982) coined the 'member-vagrant hypothesis', which suggested that recruitment variability is defined by oceanographic processes where vagrants, or "members" placed in unfavourable environments, had decreased probability of survival. The overall abundance in a patch in this case is not food limited but instead defined by the scale of the oceanographic processes that create spatial structure. Bakun (1996) proposed the 'ocean triad' hypothesis where enrichment, concentration processes, and retention mechanisms facilitate suitable nursery habitats. Bakun's triad places a particular focus on circulation as a key element in retention (Miller et al. 2006), and has been used to describe sub-population structure in European anchovy (Agostini and Bakun 2002). The "stable ocean hypothesis" (Lasker 1978), suggests that larval survival rates are positively related with vertical stratification, which increases prey abundance around

pynoclines and thus enhance larval survival rates. The stable ocean hypothesis focuses on processes similar to the second tenet of Bakun's (1996) ocean triad hypothesis, emphasizing the physical environmental link between recruitment and spatial heterogeneity in marine systems. Both predator and prey are often subject to the same oceanographic conditions leading to divergent or convergent processes impacting survival. These oceanographic conditions can place larvae to optimal food conditions but might too also converge with predators leading to decreased larval survival (see Pepin et al. 2002; 2003). These diverse hypotheses and findings clearly illustrate the importance of biological-physical interactions in regulating recruitment processes which, in turn, impact realized connectivity and spatial heterogeneity.

The influence of the physical environment on the scale of passive egg dispersal

Circulation is intrinsically related to the movement of passive particles through space and time which, in turn, can determine scales of connectivity. Circulation patterns dictate the spatial scale at which observed population structure operates (e.g., local bays, coastal areas, broad shelf). Indeed, circulation can define spatial structure and dispersal during the early life history of organisms (Laprise and Pepin 1995; Cowen et al. 2006), acting as a dispersal pathway or barrier (Gaines et al. 2007). It has long been acknowledged that understanding dispersal requires information on local circulation patterns (reviewed by Brickman et al. 2007). Detailed circulation models give researchers estimates of ambient flow conditions, which can be used to forecast patterns of eggs and larvae through space and in some cases time (Panteleev et al. 2004).

Circulation models can be applied to passive drift studies on a spectrum of spatial scales. On large (100's of km) scales, variability in year class strength of plaice (*Pleuronectes platessa L.*) has been linked to variable circulation in the southern North Sea (Van der Veer et al. 1998), and mesoscale physical processes in the central Cantabrian Sea have been shown to strongly influence larval fish retention and survival (González-Quirós et al. 2004). Davidson and deYoung (1995) suggested that inshore branches of the Labrador current transport eggs and larvae spawned offshore in the north into southern, inshore embayments, thereby acting as a possible transport vector between spawning stocks and suitable nursery areas. Discrete spatial structure of Atlantic herring stocks are maintained by a combination of optimal spawning time, which results in shorter or longer pelagic larval durations, and transport by eastern Atlantic currents (Iles and Sinclair 1982). Several studies of Georges Bank have linked specific oceanographic features to retention or advective loss of cod and haddock eggs and larvae (Page et al. 1999; Lough et al. 2006). Kloppmann et al. (2001) determined that the spatial persistence of a population of European blue whiting (*Micromesistius poutassou*) was facilitated by spatially and temporally persistent Taylor column formations in the waters over Georges Bank, which enhanced egg retention. In Alaska's Shelikof Strait, persistent circulation patterns contribute to the fragmented spatial structure of the early life history stages of walleye pollock (*Theragra chalcogramma*) (Stabeno et al. 1996). These examples of large-scale circulation patterns underpin how physical processes can be vital to connectivity among spatially extant populations, especially for the passive early life history stages of marine organisms.

On small scales (<100 km) many studies have linked local circulation patterns and egg and larval spatial patterns. For example, James et al. (2002) demonstrated that circulation over the Great Barrier Reef flushed many of the spawned eggs, leading to less self recruitment than was suggested by Cowen et al. (2000) for Caribbean reefs. Appropriate temporal and spatial placement of propagules can lead to retention to nursery habitat within Placentia Bay, Newfoundland, however, mean circulation can flush larvae from the bay if the spatial/temporal optima are mismatched (Bradbury et al. 2000; 2003). Pepin et al. (1995) noted that the influence of physical processes on mortality and flushing from Conception Bay, Newfoundland was variable and recommended cautious interpretation of the role of physical transport. Similarly modelling work by Helbig and Pepin (1998 a,b) further highlighted the importance of interactions between the scale of sampling and oceanographic processes in the interpretation of key factors influencing connectivity such as mortality. As with the large-scale processes described earlier, these examples of local processes demonstrate how even small-scale (<100km) physical processes can play a significant structuring role in observed biological patterns.

The spectrum of scales over which dispersal and connectivity occur has ramifications for the application of metapopulation concepts (Karlson 2006; Gaines et al. 2007). As connectivity increases, the spatial structure of a metapopulation decreases (Hanski 1989). For example, connectivity among multiple coastal "bay" subpopulations might be sufficiently strong that the populations respond and function as one autonomous unit. In this case, a metapopulation framework is inappropriate, at least at the spatial scale of the "bay" (Grimm et al. 2003). In terms of persistence, the "openness" of a population is

critical to how much self-recruitment occurs relative to dispersal to other populations, thus determining the degree to which a population is panmictic and resilient to local extinction (Hanski 1989). Full evaluation of connectivity and spatial heterogeneity of adult populations will help to identify the ecologically-relevant scales at which dispersal offsets mortality associated with local environmental conditions (Cowen et al. 2006, 2007) and, therefore, how subpopulations link to a larger metapopulation.

The biological-physical linkages regulating active dispersal

The larval dispersal phase is a crucial element in recruitment variability and has the potential to contribute to connectivity among spatially-distinct populations. Laboratory studies (Bellwood and Fisher 2001; Clark et al. 2005, Guan et al. 2008), and field analyses (Bradbury et al. 2003; present study Chapter 3) suggest that larval swimming behaviour has the potential to influence dispersal trajectories significantly. Even simple behaviours can influence dispersal, producing patterns that differ drastically from those predicted by a passive null model (Gawarkiewicz et al. 2007). In a review of the published literature, Cowen et al. (2006) argued that the early onset of active larval movement has a major influence on the dispersal potential of reef fish. Several studies have demonstrated that pre-settlement fishes are competent swimmers (Stobutzki and Bellwood 1997) and exhibit strong swimming directionality (Leis et al. 2007) that can facilitate retention on reef systems (Leis et al. 1996, Wolanski et al. 1997). Bradbury and Snelgrove (2001) reviewed the broad topic of larval dispersal and concluded that active swimming behaviour could play a significant role in dispersal. Stabeno et al. (1996) argued, in their analysis of larval Alaskan walleye pollock patch dynamics, that larvae

maintain spatial structure by active swimming at 5-6 weeks post hatch. Determining when and to what degree larval behaviour influences dispersal has the potential to increase accuracy of dispersal predictions relevant to population models.

In addition to passive processes, the physical environment has a significant structuring role in how behaviour can mediate dispersal. When a larval fish swims, it interacts with the fluid medium around it and is therefore bound to the mechanical principles defined by that fluid environment. To understand how the shape and motion of larvae impacts swimming performance, information is needed on how the fluid environment influences thrust and drag forces (Webb 1984; McHenry et al. 2003). Of particular relevance to larvae is how ontogeny relates to the hydrodynamic environment, in that size and shape are critically important to how the fluid environment defines physical boundaries to swimming (McHenry and Launder 2006). Reynolds number (Re), the ratio of inertial to viscous forces, is a dimensionless metric that has been used to quantify the physical environment or hydrodynamic regime around a swimming organism (Vogel 2003). Re values less than 20 characterize an environment where viscous drag places large physiological demands on swimming (von Herbing 2002), whereas Re values that exceed 300 characterize a swimming environment where inertial forces dominate and swimming is much more efficient (Fuiman and Batty 1997). Thus, the physical interaction between the fluid and the swimming organism limits swimming capability in low ($Re < 20$) or transitional ($Re < 300$) swimming environments (Gillis 2003).

During ontogeny, as larvae transition these hydrodynamic regimes, morphological changes occur that often drastically change swimming ability (Gillis 2003; McHenry and Lauder 2006). Within this context Webb and Weihs (1986), suggested that for multiple species of fish and assuming uniform physical limitations, growth in size reflects the hydrodynamic environment; larvae grow faster along the longitudinal axis relative to the body as a whole in order to minimize viscous drag and therefore expedite their transition into an inertial environment. This idea was only partially confirmed by Muller and Videler (1996), whose meta-analysis of published data suggested that, although most species at least partially conform to this general hypothesis and adapt directly to the larval fluid environment, others such as Atlantic cod seem to grow in a manner that optimizes shape for the inertial fluid environments they will encounter later in development (Koehl, 1996). In any case, these examples demonstrate the significant role that the aqueous environment plays in regulating behavioural limitations of swimming larvae, and suggest that the interaction between the fluid environment and the organism should be a major focus in further analysis.

Temperature, and therefore viscosity, varies both spatially and temporally. Therefore, swimming efficiency and growth may also vary accordingly. Von Herbing (2002) suggested that the impact of temperature on the fluid environment might be greater in cold ocean systems because cold temperatures result in higher kinematic viscosities, which in turn mean more viscous, lower Reynolds number environments around swimming larvae (Leis 2007). Larval swimming experiments carried out at temperatures above 15 ^{o}C suggest that the hydrodynamic environment has little or no influence on

swimming ability because even the smallest larvae operate in largely inertial environments (Wieser and Kaufmann 1998). Thus, temperature has a strong influence on the hydrodynamic environment and swimming capability, but this effect is much greater in cold water. Temperature has been shown to influence swimming performance (von Herbing 2002; Peck et al. 2006), escape responses (Batty and Blaxter 1992), and swimming-relevant growth trajectories (Green and Fisher 2004; Guan et al. 2008). These results highlight the biological-physical interplay in larval swimming and emphasize the need to address larval behaviour within a physical-hydrodynamic perspective, especially in cold ocean systems.

1.4 Partitioning the roles of passive and active dispersal in the field

"A mechanistic understanding of marine population connectivity requires resolution of the biological and physical processes involved in larval dispersal and transport"
Robert Cowen

Biophysical modelling

The difficulty in modelling marine population dynamics lies partially in the disciplinary separation that often divides biology from physical oceanography. In order to represent marine systems accurately, models must acknowledge the network of connections between biological and physical parameters (Santos et al. 2007). This acknowledgement is especially important for early life history dispersal, which has widely been accepted as a biophysical process (Fogarty and Botsford 2007; Gawarkiewicz et al. 2007; Pineda et al. 2007). Individual-based models (IBMs) take parameters from the biological environment (i.e., pelagic larval duration, mortality, swimming and swimming ability) and marry them with physical information (i.e., circulation and temperature). IBM's have

been useful in addressing a variety of ecological questions that are pertinent to dispersal and connectivity in the marine realm (Bartsch et al. 2004a,b, Miller et al. 2006). The IBM approach is particularly attractive because it accounts for individual variability and therefore provides realistic models of marine biological systems (Thygesen et al. 2007). IBM's can provide a wealth of information but they are only as strong as the data on which they are based (Peck et al. 2006). The inclusion of relationships between physical and biological environments can produce more accurate dispersal models that better represent field conditions (Leis 2007).

When does passive dispersal become active?

Models that test dispersal and connective processes are limited by the data that they include. The increased appreciation for the degree to which larval behaviour can influence dispersal (Gawarkiewicz et al. 2007) punctuates the need to determine when and to what degree larval behaviour can influence connectivity (Leis 2007) when developing connectivity models. In laboratory experiments, researchers can test quantitatively how an environmental variable - often temperature - affects swimming efficiency of developing larvae (Peck et al. 2006; Guan et al. 2008), but these experiments lack a strong connection to the physically dynamic fluid environment that larvae experience in the field (Leis and Stobutzki 1997). Empirical data derived from ichthyoplankton studies illustrate how spatial heterogeneity changes as a function of larval length (McGurk 1987; Matsurra and Hewitt 1995; Stabeno et al. 1996; Bradbury et al. 2003; Maynou et al. 2006), and this information has been used to infer that swimming behaviour is responsible for deviations from passive predictions. The transition from

viscous to inertial swimming environments might play a role in dictating when behaviour begins to mediate dispersal, and regional and seasonal temperature differences might play a key role in this transition (Leis 2007). The increasing body of research and discourse surrounding active larval behaviour suggests an active component to larval dispersal at some point in development, but assessing this possibility with an interdisciplinary approach that utilizes the methodologies discussed above may represent our best chance at predicting the transition from passive plankton to active nekton.

1.5 Summary and study objectives

"This work illuminates how empirical studies can be used to test hydrodynamic theory and explore the physical world of organisms at low or transitional Re"
Gary Gillis

Fisheries management and conservation biology share the mutual goal of understanding population persistence in a spatially heterogeneous habitat landscape. Metapopulation biology, combined with research in connectivity, offers fisheries managers and conservation biologists a mechanistic approach to understanding the processes that underlie population spatial structure and persistence (Hastings and Botsford 2006). The use of a metapopulation framework to identify key connective processes (Gaines et al. 2007), in tandem with measurements of connectivity within a biological-physical perspective, provide an invaluable opportunity to address many issues facing marine conservation and fisheries management today.

Atlantic cod (*Gadus morhua*) represents a major fishing resource for Atlantic Canadian and world markets (Hutchings and Myers 1994). However, overfishing in Atlantic Canada led to its collapse and the establishment of a fishing moratorium in 1992. Since then, despite a greatly reduced fishing pressure, the once great northern cod stock has shown little sign of rebound (Rose et al. 2000; DFO 2008) contrary to initial optimistic predictions (Myers et al. 1997). In the early 1990's a large overwintering population of Atlantic cod was discovered in Smith Sound, Trinity Bay (Rose 1996). The discovery of this large aggregation of Atlantic cod garnered interest in whether an inshore population of Atlantic cod could contribute to the recovery of offshore populations. Smedbol et al. (1998) attempted to address this question in Trinity Bay, and found no detectable increase in age 0 cod as a result of increased spawning biomass in Smith Sound. Continuing research in Smith Sound has noted significant annual spawning activity from this large aggregated biomass (Rose 2003), which was recently estimated at 14,000 tonnes (DFO 2008). Given its temporal persistence, increased understanding of egg and larval transport from the sound is of great interest, and might help explain the counterintuitive findings of Smedbol et al. (1998). Documentation of connectivity of Smith Sound cod with adjacent waters will also provide important insight into the larger-scale population structure of inshore (and perhaps offshore) Atlantic cod.

The dynamic physical environment into which propagules are spawned has the potential to greatly influence connectivity and dispersal (Bradbury et al. 2001, 2003). To address this influence, data are needed to characterize the physical and biological processes that impact the study system. Moreover, there is a specific need for empirical data to confirm

the accuracy of dispersal models. For the passive dispersal phase, this type of data is necessary for quantifying biological parameters such as pelagic stage duration and mortality. Much research on active dispersal has been focused on laboratory studies and on tropical coral reef systems. For cold ocean species, there are limited field data from which to infer behavioural contributions to dispersal and connectivity. Complementary studies that consider the spatial and temporal movement of spawning propagules and associated local environmental conditions are needed to illustrate connectivity accurately and understand its possible role in larger-scale questions on population level processes.

Chapters 2 and 3 address key issues indentified in this chapter by modeling dispersal from the Smith Sound spawning aggregation with empirical field data. Chapter 2 addresses the influence of spatial and temporal placement of propagules in the Smith Sound system and models their movement as they are flushed into the larger Trinity Bay system. Chapter 2 provides empirical evidence that illustrates the movement of eggs and larvae and addresses how connectivity and Smith Sound may contribute to fragmented inshore and offshore systems. Chapter 3 specifically addresses the potential role of larval behaviour in dispersal, and evaluates relationships between the physical environment and active swimming in light of field distribution data. Both chapters address connectivity with empirical catch data and field observations on physical variables. Collectively, these chapters address the interplay between the physical environment, swimming, and dispersal, and the relevance of spawning from Smith Sound to larger spatial population dynamics.

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Chapter 2 Scales of Connectivity for Atlantic Cod Spawning in Trinity Bay, Newfoundland

2.1 Introduction

Atlantic cod, was the mainstay of the economy and culture of the Northwest Atlantic for over 350 years before overfishing pushed the northern stocks of this species to near eradication by the early 1990s (Rose 2007). In a time span of less than 35 years the 2J3KL cod stock, which represented the core of the northern cod population, was reduced from 3 million tonnes to less than 80,000 tonnes (Sinclair, 1996). The drastic collapse in cod stock biomass spurred the implementation of a fishing moratorium in 1992 (Lear and Parsons 1993) in an attempt to allow the dwindling population to rebuild. However, even with a 16-year absence of directed fishing effort, there has been no clear sign of recovery to the offshore stocks (Rose et al. 2000; DFO 2008), despite optimistic predictions to the contrary (e.g. Myers et al. 1997).

With the cod stock at crisis levels, considerable research effort has been directed towards understanding the structure and function of current cod stock so that effective management frameworks can be established (Taggart 1997). In the late 1990s surveys indicated that offshore 2J3KL stocks remained at extremely low levels, < 8%, (DFO, 1998) and much of the remaining biomass of cod was distributed within coastal bay habitats (Rose 1992, Smedbol and Wroblewski 1997). Traditionally the northwest Atlantic cod complex was viewed as a mixture of offshore and inshore components (Hutchings et al. 1993) where cod overwintered and spawned offshore and circulation patterns delivered eggs and larvae into nursery areas in coastal embayments (deYoung

and Rose 1993; Pepin and Helbig 1997). During the summer many offshore cod would migrate to coastal areas in search of capelin, thus mixing with the smaller resident inshore cod population (Pinhorn 1984). As a result of this mixing the two stocks were often combined in management scenarios, with priority consideration for the main offshore resource (Wroblewski et al. 2005).

In the mid 1990s, a large spawning aggregation of approximately 17,000 tonnes (DFO 1998), was located in Smith Sound on the western side of Trinity Bay Newfoundland (Wroblewski et al. 1994, Rose 1996, Smedbol et al. 1998). The observation that this overwintering aggregation remained inshore year round and represented the majority of the remaining 2K3KL cod biomass (Rose 1996), sparked interest in the potential role that inshore spawning events might play in any recovery of offshore stocks (e.g Smedbol and Wroblewski 1998, Wroblewski et al. 2005). Moreover, new genetic data at the time, that demonstrated spatial structure in the remaining stock (e.g. Ruzzante et al. 2000, 2001). Collectively, this evidence underscores the need for spatially-oriented conservation and management strategies (e.g. Fogarty and Botsford 2007) in order to facilitate long-term recovery of offshore stocks and sustain the remaining inshore population (Smedbol and Wroblewski 1998).

The use of marine metapopulation models offers great promise for better understanding of population spatial structure and its application for marine management (e.g. Cowen et al. 2007, Gaines et al. 2007). The heterogeneous mosaic of sub-populations within and between bays in coastal Newfoundland (Ruzzante 2000, 2001) is maintained through

dispersal, the magnitude of which is defined as connectivity (Bradbury et al. 2008). The egg and larval dispersive stages represent an opportunity for connectivity between spatially extant population sub-units (Cowen et al. 2006) and is often the defining life history stage for population structure (Harden-Jones 1968; Cowen et al. 2000).

Several studies have considered the function of inshore populations, particularly Smith Sound, to the 2J3KL cod stock complex. Wroblewski et al. (2005) suggested that the coastal environment might represent a "heartland" where outmigration from the optimal coastal habitat to offshore habitats was dependent on cod density inshore; at some threshold density, a subset of individuals would begin to migrate to offshore overwintering and spawning grounds, similar to what Rose (1996) suggested earlier. A comprehensive understanding of connectivity from the inshore stock complex during the early life history is fundamental to any metapopulation model and its application to understanding how the inshore population might contribute to any offshore recovery.

Smith Sound represents a unique opportunity to explore connectivity of early life history stages of Atlantic cod that originate from a discrete inshore spawning event in a spatially distinct area. Smith Sound fjord is relatively small (~36 km^2) and geographically bounded by land on three sides, resulting in a natural system in which eggs and larvae disperse from a defined point source (Smedbol et al. 1998). Although Smith Sound supports the largest known remaining aggregation of Atlantic cod in the 2J3KL stock complex (Rose 2003), previous work in the area did not detect any significant signal of increased age 0 cod settlement or linkage between early life history densities and the Smith Sound

biomass spawners (Smedbol et al. 1998). These results bring into question the biological-physical linkages that define connectivity of Smith Sound with surrounding Trinity Bay and the larger scale 2J3KL population.

My study addresses two questions relating to dispersal and connectivity within and beyond the Trinity Bay system: 1) What are the dispersal characteristics of eggs and larvae spawned from Smith Sound and how might this vary seasonally? 2) How might the early life history of Atlantic cod play a role in the relationship between the Smith Sound aggregation and the larger 2J3KL stock complex? I address these questions through a derivation of dispersal with empirical data fitted to a variety of biophysical model scenarios. The results from this study offer insight into the possible linkages between inshore and offshore stocks as well as a better understanding of linkages that define the current 2J3KL inshore stock.

2.2 Methods

Study Area

Trinity Bay (48° 2'N, 53° 25'W) is a coastal embayment on the northeast coast of Newfoundland with an approximate surface area of 3870 km^2 (Figure 2.1a). The bay widens to ~29 km wide at the mouth, with a length of 100 km along the longest axis which is oriented 30 degrees east of north. A trench on the western side and a sill on the eastern side of the bay are 350 m and 150 m deep respectively. Circulation modelling by Yao (1986) and Tittensor et al. (2001; 2002) illustrates that circulation patterns are strongly influenced by an inshore branch of the Labrador Current. Current meter

observations indicate that the mean flow direction is typically equal to the variance (Tittensor et al. 2001; 2002). Nonetheless, there is a clear pattern of water entering on the west and exiting on the eastern coast is evident. Flow variability, primarily driven by wind stress (Davidson et al. 2001), produces complex patters of current response dominated by a complex upwelling-downwelling cycle and a Kelvin wave response. A counter clockwise gyre can also be observed near the mouth of Smith Sound, exhibiting some strong flow (Figure 2.2, from Tittensor et al. 2002). Passive residency times in Trinity Bay, based upon particle tracking calculations using the Candie model (Davidson et al. 2001), are on the scale of days to weeks (B. deYoung, personal communication, Department of Physics and Physical Oceanography Memorial University of Newfoundland, St. John's NL, A1C 5S7).

Smith Sound is one of two fjords that border Random Island, a large island on the western side of Trinity Bay, 40 km from its mouth. The sound is approximately 1.8 km side and 20 km long, with trenches in excess of 350 m depth and sills as shallow as 150 m. Smith Sound is of particular relevance because it is the overwintering location for the largest known spawning aggregation of Atlantic cod in the NAFO 2J3KL cod complex (Rose 1996, 2003).

Biological sampling

To estimate temporal characteristics of egg release by spawning cod, high-frequency ichthyoplankton samples (~ bi-weekly) were obtained from ring net surveys at six stations in Smith Sound (Figure 2.1c) from April to June in 2006 and from March to August in

2007. This timing was chosen to capture the majority of spawning activity from the Smith Sound cod aggregation and provide information needed to forecast developmental trajectories. Ichthyoplankton samples were obtained with a 1-m diameter by 3-m long ring net fitted with 333 µm mesh. Sample volumes were calculated from a General Oceanic flowmeter (Model 2030R) secured in the centre of the ring net mouth. Ring nets were towed at the surface at approximately 3.7 $km \cdot h^{-1}$ (2 knots) for 20 minutes towed at the surface. Vertical distributions of CHW eggs have been shown to vary as a function of water density, egg density and developmental stages (Anderson and deYoung 1994; 1995). Salinity data for the surface layer was not collected concurrently with ring net samples because of logistical constraints, however, data on salinity collected during Tucker trawl surveys (described below) show that salinity does not varies less than 0.1 among all surveys. Because variability in salinity is low, I do not expect the catchability of any egg stages to change within and among sample surveys.

In addition to ring net surveys in Smith Sound synoptic ichthyoplankton surveys of Trinity Bay provided a basis to infer dispersal trajectory and spatial pattern of propagules produced by spawning events in Smith Sound. During the spring (May of 2004 and 2006) and summer (July 2004) ichthyoplankton was collected from the CCGS Shamook over a grid of twenty stations. These surveys were performed in duplicate for spring surveys and triplicate for the summer survey. The sampling grid was comprised of three stations within Smith Sound and three concentric rings that radiated outward from Smith Sound with radii of approximately 5, 10, 20 and 30 km from the mouth of the sound (Figure 2.1b). Double oblique tows were carried out using a 2.0 m by 2.0 m Tucker trawl fitted

with decreasing mesh sizes of 1000, 570, and 333 µm progressing from the front of the net to the cod end. The trawl was lowered to a maximum depth of 40 m and towed at ~3.7 knots for 20 minutes. Volumes sampled were calculated using the maximum sample volume recorded by either of the two General Oceanic flowmeters (Model 2030R) mounted at the mouth of the net. The maximum value obtained from the flowmeters was used because it is much more likely that flowmeter rotations will be underestimated (e.g. tangling, twisting, jamming) than overestimated; other than some additional rotations during deployment it is difficult to envision how an overestimate it possible. The upper 40-m depth range has been shown to encompass >95% of the ichthyoplankton species by several studies in coastal Newfoundland (deYoung and Rose 1993; Laprise and Pepin 1995) and is occupied by positively buoyant fertilized eggs of Atlantic cod (Saborido-Rey et al. 2003). Tucker trawls are effective samplers of egg and larval life history stages from a multitude of fishes, and produce much less sample variability compared to other ichthyoplankton sampling gears (Pepin and Shears 1997).

All ichthyoplankton samples were preserved in 4% formalin in buffered sea water. In the laboratory, all fish eggs and larvae were removed and identified except where egg stage and larval abundances for a given taxon exceeded 300 individuals, in which case they were sub-sampled using a Motodo plankton splitter. Eggs of all species were grouped into four taxonomic development stages (Table 2.1.) adapted from methods outlined in Markle and Frost (1985). Eggs identified as the "CHW" complex could represent Atlantic cod (*Gadus morhua*), haddock (*Melanogramus aeglefinus*), or witch flounder (*Glyptocephalus cynoglossus*) because these species are indistinguishable based on

morphology during the initial egg stages. Previous work in the area assigned all of the CHW eggs to Atlantic cod (Smedbol et al. 1998), which is reasonable given low abundances of late egg stages and larvae of both haddock and witch flounder relative to cod, and the large spawning aggregation of Atlantic cod that occurs in Smith Sound. The majority of CHW eggs were therefore assumed to be from Atlantic cod with small undetermined proportion of haddock or witch flounder eggs. Samples from May 2006 were also processed for zooplankton abundances (St. Germain 2007) following sub-sampling protocols outlined for the CHW eggs according to the lowest taxonomic level identifiable.

Physical observations

Temperature was the key linking variable in modelling scenarios for biological observations in the field. Continuous temperature data for Smith Sound was derived from temperature loggers secured at depths ranging from 10 – 40 m collected during the spring and summer from 2004-2007 (Figure 2.1c). Vertical CTD casts for conductivity, temperature, and depth (SeaBird Electronics SBE 19) were collected with each ichthyoplankton tow during the Trinity Bay Tucker Trawl surveys, providing physical data on the surface and mixed layers for Smith Sound and Trinity Bay. Measurements were divided and compared among eastern and western Trinity Bay as described above for the biological measurements.

Data analysis

Egg number collected at each station was standardized by sample volume and expressed as CHW eggs•1000 m^{-3}. Spatial distributions of total concentrations of egg and larvae as well as different stages were plotted using linear kriging in Surfer® 8 to interpolate total concentrations between sample stations. Linear kriging provides a spatial estimate of biomass using data interpolated from all stations sampled. This method removes spatial bias that might result from the closer spacing of sample stations with increasing proximity to Smith Sound and is therefore more appropriate than other contouring methods available (Papritz and Stein 1999). Kriging output for Trinity Bay were divided into eastern and western groupings based on output GPS coordinates that split the bay down the central axis. Statistical comparisons between eastern and western Trinity Bay were based on the General Linear Model (GLM) analysis of variance in SPSS 16.0.

Spatially referenced kriging data were also utilized to calculate the "centre of mass" (COM) of each egg stage within a particular survey according to:

$$COM_Z = \frac{\sum(D_i Z_i)}{\sum(D_i)} \quad (1)$$

where COM_Z is the calculated centre of mass along either the latitudinal or longitudinal axis for a given latitude or longitude Z_i, for station i, and D_i is the observed concentration at the i^{th} station. Output from linear kriging analyses provided a mechanism to avoid or at least minimize spatial bias associated with the expanding circle sampling array by reducing the relative impact of closely-spaced stations (Figure 2.1b).

Distances between COMs of each egg stage were used to infer passive transport rates. According to the following equation:

(2) $$v = \frac{d}{t}$$

where v is the estimated transport rate, d is the distance, determined via great-circle calculation, between centre of mass estimates and t is the difference in duration between CHW egg stages 1-2 and 3-4 according to temperature dependent stage duration equations derived from Bradbury et al. (2001). Temperature data used in this analysis was derived from survey average CTD cast data, at the surface (10 m) and mixed layer depths (40 m). To account for variability in the calculation of mean at depth temperature, and therefore passive pelagic duration, 1000 Monte Carlo randomizations were performed in Matlab using the maximum and minimum observed temperatures as boundaries. These 1000 randomized mean temperatures were then used to calculate the variability of possible transport distances given observed data. These estimates of error enable a realistic comparison of transport distance variability based on real data and are independent of any specific statistical error structure.

Egg concentration is expected to decrease as a function of distance from Smith Sound as a result of both mortality and diffusion. To account for the effect of diffusion, egg concentration was calculated according to:

(3) $$N=CDA$$

where N is the number of eggs, C is the observed concentration of eggs, D is the mixed layer depth (~40 m) and A is the radial surface area. Radial surface area is calculated

based on the surface area of an arc sector increasing in diameter at 1 km distance intervals radiating out from a vertex at the mouth of Smith Sound (53.54 ^{o}W 48.22 ^{o}N). The boundaries of the sector arc were taken as the station locations that were furthest north-west and south east (approximately 53.20 ^{o}W 48.35 ^{o}N and 53.56 ^{o}W 47.97 ^{o}N, respectively). Mean egg concentration and variance in egg number could then be calculated as a function of distance from Smith Sound. The great-circle distance calculation was used to calculate distance between GPS coordinates and associated concentration estimates; the great-circle provides the best estimate of distance between two points taking advantage of the known radius of the Earth (6371 km).

Modelling

To estimate parameters of spawning and dispersal from Smith Sound, I created a two-box model in Matlab. The primary model considered only data from Smith Sound (Figure 2.3 a). Eggs are released, experience mortality, and progress through egg stages each time step (daily). In the primary model, which represents Smith Sound alone, mortality is the combined effect of loss due to death and loss due to advection from the system. For each day, the model output dictates the numbers for each egg stage that are present in the Sound based on modelling scenarios. The secondary model, which adds Trinity Bay to the primary model, estimates dispersal from Smith Sound to Trinity Bay (Figure 2.3 b). The loss component from the primary model (i.e. Smith Sound) is used as an input into the Trinity Bay system. Thus, the eggs that exit Smith Sound are an output of the primary model, and enter Trinity Bay, which is represented by the secondary model. In all modelling scenarios, daily output of the relative frequency of each egg stage was

compared to available data from the system to determine the model fit and to estimate parameters. The secondary model used only data from western Trinity Bay stations (Figure 2.1 b).

To model potential spawning dispersal from Smith Sound I created a three-vector Leslie matrix in Matlab:

(4) $$\beta = [i, j, k]$$

Where β is the three-dimensional matrix that represents Smith Sound, i is the vector tracking the cohort released over the 144 days over which egg production is inferred to have occurred, j is the vector that tracks day 1-144 and k tracks the egg stage (Stage 1-4 and larvae). Eggs are released on each day according to the different spawning scenarios where protraction of spawning and thus height of spawning peak is changed. Each day, eggs progress through a percentage of an egg stage according to the cumulative egg development durations developed from Bradbury et al. (2001):

(5) $$\text{Stage 1} = e^{[2.36+T(-0.12)]}$$
(6) $$\text{Stage 2} = e^{[3.12+T(-0.17)]}$$
(7) $$\text{Stage 3} = e^{[3.45+T(-0.15)]}$$
(8) $$\text{Stage 4} = e^{[3.65+T(-0.12)]}$$

where T is the temperature observed on the j^{th} day. Each day j_i the cohort completes a percentage of a stage as defined in equations 5-8. Once a cohort has completed 100% of a stage, it is lost from the preceding stage and begins the subsequent stage on the next day j_{i+1}. Eggs are tracked and experience mortality collectively as cohorts. Daily cohorts include the previous day's cohort minus mortality loss for that stage. Temperature data

for egg durations were derived from CTD casts utilizing both mean surface (<10m) and mixed layer depth (<40m).

Net mortality is accumulated in daily time steps according to:

(9) $$M_{net} = D + L$$

where M_{net} is the net mortality, D, the product of natural mortality from egg death and L is declines resulting from transition out of the k^{th} stage or passive diffusion out of Smith Sound. The $Mortality_{loss}$ term from the Smith Sound model was subsequently used as in input term into the adjacent zone, $Trinity\ Bay_{west}$ (Figure 2.1b). Several hypotheses could then be explored with the model by varying model inputs and comparing predictions against empirical data derived from Smith Sound and Trinity Bay empirical surveys.

What temporal spawning pattern best fits observed Smith Sound data? What is the best estimate of net mortality in Smith Sound? Spawning temporal characteristics were modelled using several theoretical Gaussian spawning scenarios, and an empirically-derived spawning model based on observed temporal patterns in egg abundance. This model compared a total of six normalized Gaussian spawning scenarios that varied in degrees of protraction (Figure 2.4). The peak egg abundance predicted by the Gaussian curves was set to coincide with the peak mean abundance observed in the Smith Sound surveys. All spawning scenarios encompassed the observed spawning activity from March 30th to August 20th. The Smith Sound model was run with spawning scenarios as variable inputs of eggs over the spawning period. Within each spawning scenario, model run net mortality was also varied from 0-100%. During a model run, the final output is a

distribution of egg stage counts for each of the daily time steps during the designated period (March 30th to August 20th). Because egg numbers could not be reasonably estimated given the data limitations, the model output was presented as the relative frequency of each egg stage per day. The model output was truncated to days where Smith Sound survey data was available.

To account for variability from ichthyoplankton surveys in Smith Sound (5 stations, Figure 2.1 c), a Monte Carlo randomization, using mean egg stage concentration ± 1 standard deviation as limits, was used to compute 1000 mean abundances of each egg stage on each sample day. The survey randomization data was then transformed into relative frequencies of each egg stage on a given day. Model output was compared to survey data individually for each egg stage. The relative frequency of an egg stage for each day sampled was regressed against model output for the observed days, producing a coefficient of determination (r^2). The fit of the model was determined by calculating the mean r^2 minus the variance in r^2 for a given spawning scenario treatment and mortality rate. This method maximized the model fit to all egg stages, and avoided erroneous parameter estimates confounded by strong fits to some stages and weak fits to others.

When the model finished all permutations each model treatment was left with a 1000 estimated model fits. The total model fit was assigned to each model treatment (given spawning scenario and mortality) using the same algorithm stated above using the calculated model fits (1000). Total model fit was then plotted against mortality treatment for each spawning treatment (Figure 2.5). The spawning treatment, and corresponding net

mortality, with the highest model fits represent the best estimation of Smith Sound data. The analysis was repeated using observed surface (10 m) and mixed-layer (40 m) temperatures. Although the mixed layer has been shown to contain ~95% of the ichthyoplankton (deYoung and Rose 1993; Laprise and Pepin 1995) some evidence suggests that the positive buoyancy of eggs can lead to higher abundances at the surface (Pepin et al. 2005; Pepin et al. 2007). The utilization of both surface and mixed-layer temperatures provides a mechanism to account for any predicted vertical structure.

Does variable mortality for each egg stage improve model fit?

To determine whether the probability of loss is stage-dependent, and noting that the longer an egg remains in Smith Sound and develops to later stages, the greater the likelihood of advective loss, $\text{mortality}_{\text{Net}}$ was broken down into components $\text{mortality}_{\text{Natural}}$ and $\text{mortality}_{\text{Loss}}$. In this simulation the $\text{mortality}_{\text{Loss}}$ term was broken down into the sum loss of all egg stages which, in turn, is equal to the difference between total $\text{mortality}_{\text{Net}}$, estimated as:

(10) $$M_{\text{Loss}} = M_{\text{Net}} - M_{\text{Death}}$$

$$L = \text{Stage 1}_{\text{Loss}} + \text{Stage 2}_{\text{Loss}} + \text{Stage 3}_{\text{Loss}} + \text{Stage 4}_{\text{Loss}}$$

Loss rates for each term were created based on a multiplication factor (increasing probability of loss as eggs progress through stages) from the estimated loss of the previous stage so that the likelihood of egg stage loss increases with pelagic duration. Thus:

(11) $$L_i = 1 + \alpha L_{i-1}$$

where L_i is the loss rate for the associated stage and 'α' is the multiplication factor. A string of multiplication factors (0.01-1) were tested in consecutive model loops. These multiplication factors were set as numerical parameters to augment the loss of an egg stage relative to the previous stage (i.e for a α of 1 and stage 1 loss set at 0.05 the mortality preceding three stages would equal 0.1, 0.2, and 0.4 respectively). Resulting model fit scores were recorded after each loop and compared to the single loss rate (L) to determine whether varying the loss rate for each egg stage improved the fit for the estimate of Smith Sound net mortality in Smith Sound..

What is the best estimate of daily egg loss from Smith Sound? $\text{Mortality}_{\text{Loss}}$ (L) can be inferred from difference between $\text{mortality}_{\text{Net}}$ (M_{net}), estimated as described above, and $\text{mortality}_{\text{Natural}}$ (D) derived from empirical data according to the equation:

$$D = \frac{\ln(\frac{N_1}{N_o})}{(t_1 - t_0)} \quad (12)$$

where N_o and N_1 are the combined mean survey abundances for consecutive stages and t_o and t_1 are the predicted egg stage durations. To account for variability in abundances among Trinity Bay stations, abundance and temperature data from each survey were bootstrapped 1000 times to estimate a mean mortality rate and a standard deviation. $\text{Mortality}_{\text{Natural}}$ estimates were also derived from the literature and ranged from 0.1/day to 0.3/day (Campana et al. 1989; Sundby et al. 1989; Heath 1992; Bradbury et al. 2001; Panteleev et al. 2004; Mountain et al. 2008).

Survey data from western Trinity Bay (Figure 2.1) stations offered a means to compare estimated loss rates with real observations in the field. Because survey data from Trinity Bay was collected with Tucker trawl gear and Smith Sound survey data was collected with ring nets, absolute concentrations could not be compared. Instead, as with previous simulations, data was transformed into relative frequencies of each egg stage. In order to estimate egg loss from Smith Sound, the model was run with varying degrees (1% increments) of loss up to and including the total net mortality estimated for Smith Sound. Each treatment loop was compared to data from Trinity Bay Tucker trawl ichthyoplankton surveys. Estimates of loss rates were ranked individually for each survey and survey round by minimizing the sum of squares difference among relative frequency of each eggs stage. The ichthyoplankton surveys from 2004 provided sufficient temporal data to fit a seasonal loss rate. Coefficients of determination values and model fits were calculated between truncated 2004 ichthyoplankton sample and model data for respective sample days, using the same spawning scenario fits described above.

Ichtyoplankton data can be extremely variable in that even small-scale processes can greatly impact egg abundances in the field (Helbig and Pepin 1998 a,b; 2002). To account for the variability in Trinity Bay egg concentrations, relative frequencies and mean abundance were calculated from 1000 randomizations for each loss treatment. As in the simulations described above, the highest mean r^2 for each egg stage minus the variance for the 1000 randomization loops was deemed the best model fit for each treatment and the best estimate of loss from Smith Sound to Trinity Bay. Model results can be represented by the following (8,n,1000) matrix:

(13) $$\beta = |i, j, k|$$

where i denotes the individual survey rounds (7 rounds total) plus the combination of all survey rounds in 2004 is the number of mortality treatments defined by results in question 2 (n=mortality$_{Net}$*100), j is the number of mortality treatments defined by results in the analysis of daily egg loss (n=mortality$_{Net}$*100), and k represents 1000 model fits estimated from the data randomizations. For each survey (i) and corresponding mortality (j), 1000 model fits were calculated. As in previous models, the total model fit was computed from the 1000 Monte Carlo randomizations according to the mean model fit minus the variance observed in the randomizations. The most appropriate loss rate can then be considered the best total model fit for a given survey (Figure 2.6).

2.3 Results

Field observations

Mean concentrations of stage 1 CHW eggs were highest in Smith Sound during early summer (particularly early July 2007). Increases in egg concentrations through June and July also coincided with increases in mixed-layer temperatures (Figure 2.7). Abundances of stage 1 CHW eggs, relative to all other stages, in Smith Sound were negatively correlated with mixed-layer temperature among sample years (Pearson correlation = -0.368, p=0.041, n=29; controlled for year).

The highest concentrations of early CHW egg stages (1-2) were closely associated with Smith Sound, the assumed natal source. Late stage CHW eggs (3-4) were typically most abundant in the western inner portion of Trinity Bay, as would be predicted from mean

southerly transport once eggs are flushed from Smith Sound. The observation for stage 1 eggs was consistent among all surveys whereas the spatial locations of late stages, particularly stage 4, were much for variable (see Figures 2.8-2.10 for May 2004, July 2004 and May 2006 respectively). Egg concentrations from the July 2004 survey were the highest observed among all Trinity Bay Tucker trawl surveys, which was consistent with temporal spawning data from Smith Sound. In all surveys, the western side of Trinity Bay had significantly greater concentrations of egg stages (GLM egg density, side of bay, $survey_{covariate}$, egg $stage_{covariate}$, F= 34.743, 16.306, 3.433, 84.490; df=3,1,1,1; p= <0.0001, <0.0001, 0.064, <0.0001) Larvae were also significantly more abundant on the western side of Trinity Bay (based on 95% confidence intervals, Figure 2.11).

Egg numbers were unrelated to distance from Smith Sound. Regression analysis demonstrated that egg number was effectively constant (slope =0.021, f=11.048, r^2 = 0.062, p = 0.001, df_{tot} = 167) as a function of distance from Smith Sound for all surveys where egg stage was a significant covariate. Overall there is a large degree of variability in egg number as a function of distance from Smith Sound and no consistent pattern was observed among all surveys. There was also no significant trend in distance from Smith Sound and variance in egg concentrations (f=0.225, p=0.636, df_{tot}=167) for individual or pooled surveys.

Evidence of upwelling was observed on the western side of Trinity Bay north of Random Island (Figure 2.12), during all of the sampling periods in spring and summer, which was consistent with previous studies in the area (Yao 1986; Schillinger et al. 2000; Davidson

et al. 2001; Tittensor et al. 2001, 2002; Baumann et al. 2003). This upwelling region was also characterised by significantly higher primary productivity levels (fluorescence) and zooplankton abundance (Table 2.2).

Centre of mass (COM) calculations indicate a general south-easterly progression between early (1-2) and late (3-4) CHW egg stages (Figure 2.13). The longest observed distance between early to late COM calculations was in May 2006 with a mean distance of 7.6 km (s.d. = 0.3). Distances were less for July 2004 (2.8 km, s.d. = 0.5) and May 2004 (3.0 km, s.d. = 2.4) respectively. The shortest COM distance was in the first survey of July (0.2 km) but subsequent survey rounds during the same cruise produced a mean distance of 4.4 km (s.d. = 0.3). Centre of mass calculations tend to be conservative because variance for weighted mean latitude and longitude calculations are not calculated and symmetrical bidirectional dispersion will be artificially masked by the calculation. However observations of spatial data (Figures 2.8-2.10) and COM locations do not suggest such an underlying pattern. Despite the conservative approach this calculation offers, I believe the patterns explained from these data sufficiently explain the mean conditions in the field.

Estimates of passive transport distances were made based on calculated Euclidian distances between centre of mass and development rates predicted from average temperature readings during the same survey. Based on 1000 bootstrapped mean temperatures, the estimated mean passive transport among all surveys was significantly greater using mixed-layer temperatures (0.43 $km \bullet day^{-1}$,s.d. = 0.25) than estimates based on surface temperatures (0.32 $km \bullet day^{-1}$, s.d. = 0.18) ([GLM, $p<0.0001$, $F=1020$,

df_{tot}=13999]). This finding was expected given warmer surface temperatures and projected faster development rates. Both distances are consistent with the limited data on mean currents in Trinity Bay (see Tittensor 2001, 2002).

Model results

What temporal spawning pattern best fits observed Smith Sound data? Model simulations indicated that the most protracted spawning scenarios produced the best fit (mean - variance) for the 1000 randomizations of survey data for both mixed-layer and surface-layer temperatures (Figure 2.14). The weakest predictive capability in both temperature treatments (surface and mixed-layer) was the empirically derived bi-modal distribution. When comparing mean field data for all stages, the Gaussian 25 (mixed) distribution produced the overall best predictive capacity, explaining 73% of the variance in the model. The Gaussian 25 (mixed) distribution was therefore used for the remainder of the modelling analyses.

What is the best estimate of net mortality in Smith Sound? Does variable mortality for each egg stage improve model fit? Net mortality in Smith Sound was estimated to be 27%, and explained 73% percent of the variance for relative frequencies of each stage on different $days_{obs}$. The model fit was improved when a multiplication factor ('α') was used therefore increasing the probability of advective loss for sequential egg stages. The improvement in model fit continued until the multiplication until 'α' approached 1.2. The best model fit for all eggs stages was obtained when 'α' was set at 0.55, which explained 79% of the variance in Smith Sound data. Based on these results, a stage 4 CHW egg was

~4 times more likely to have been flushed from the Smith Sound system compared to a stage 1 egg. Even though there were differences in egg stage mortality (largely based on their relative durations) the overall net mortality in Smith Sound remained at approximately 27% .

What is the best estimate of daily egg loss from Smith Sound? Natural mortality estimated from field egg stage abundance data estimates daily natural mortality (death) at ~0.07 (s.d. = 0.01) based on 1000 bootstrap iterations of equation 9. In contrast with the mortality estimate above, models compared with Smith Sound ring net survey data suggested that net mortality within the sound was approximately 0.27, explaining approximately 73% of the variance in the data among stages (Figure 2.15). With this estimate of net mortality the daily loss from Smith Sound would be ~20% ($Mortality_{Loss}$ = $Mortality_{Net}$ – $Mortality_{Natural}$).

Loss rates estimated from western Trinity Bay data ranged from 2-15%/day for individual surveys and were significantly positively correlated with day of year (GLM, f=64.689, $p<0.0001$, df_{tot} =6999) (Figure 2.16). The average loss rate estimated from all individual survey estimates was 10.3%/day (s.d. = 7.7%). Standard deviation associated with mean estimates of loss demonstrated no significant trend with day of year (GLM, f=4.616, $p=0.084$, df_{tot} =6). In 2004, there were sufficient sample days to estimate the parameters for among stage model fitting that were utilized in the first and second simulations. The 2004 spawning season regression model estimated the daily loss rate from Smith Sound 13%, with higher variability (s.d. = 11%) than that found for individual surveys. Based

on all estimates of loss, derived from individual survey and annual data, the mean loss rate from Smith Sound was estimated at 9% (s.d. = 7.5%).

2.4 Discussion

Nearly all facets of marine ecology, conservation, and management require some understanding of how populations are structured and which biological processes maintain this structure. For many marine species, the early life history is a key component that sets the foundation for this structure (Harden-Jones 1967; Fogary and Botsford 2007). Connectivity offers an approach to understanding the role of passive dispersal potential during the early life history in structuring populations. For cod in the Northwest Atlantic, there has been much interest in population structure, how it is maintained, and what role inshore populations might play in any future recovery of depleted offshore fishing stocks (Hutchings and Myers 1994; Wroblewski et al. 2005). In recent years, there has been particular interest in the relationship between the large annual spawning/overwintering aggregation observed in Smith Sound (Rose 2003; DFO 2008) and the larger 2J3KL cod stock complex (Smedbol et al. 1998; Ruzzante et al. 2000; Bradbury et al. 2001; Bradbury et al. 2008). Previous work has found no link between recruitment and spawning from Smith Sound (Smedbol et al. 1998).

Much work has focussed on behavioural (Smedbol and Wroblewski 1997; Rose et al. 2000; Rose et al. 2003) and physiological (Rideout et al. 2000; Rideout et al. 2005; Rideout and Rose 2006) aspects of adult and spawning Atlantic cod in Smith Sound.

However, there is little detailed information about dispersal and connectivity of egg and larval stages dispersing from the Smith Sound, like that produced for offshore stocks (deYoung and Rose 1993) and nearby Placentia and Conception Bays (Bradbury et al. 2000 and Laprise and Pepin 1995 respectively). Empirical information about dispersal from Smith Sound will represent invaluable information about how this aggregation is sustained, what role it plays for cod in Trinity Bay, and how it might contribute to the broader scale 2J3KL cod stock complex.

Biological observations of dispersal

Observations from Smith Sound ichthyoplankton surveys in 2006 and 2007 indicate a bi-modal protracted spawning pattern that spans from March until August and peaks weakly in late May and more strongly in mid to late-July. Increases in egg production coincided with increases in temperature in late July exposing the majority of egg development to the highest expected annual temperatures (July and August). Model simulations are consistent with strong temperature dependency and protracted rather than discrete spawning scenarios. Specifically the most protracted scenario, Gaussian (s.d.= 25), provided the best fits to the empirical data. These results are similar to previous studies that have documented extended spawning in Atlantic cod (Pinsent and Methven 1997; Brander 2005) and inferred timing of Trinity Bay cod spawning from ichthyoplankton surveys (Smedbol and Wroblewski 1997). Both modelling and field data show that stage 1 CHW egg abundance is strongly and positively related to temperature (see Figure 2.7). The temperature dependence observed in this study follows previous results that suggest spawning in Smith Sound (Smedbol and Wroblewski 1997) and Conception Bay (Laprise

and Pepin 1995) is environmentally driven and related to temperature (but see Bradbury et al. 2000 regarding nearby Placentia Bay cod). Regional variation in timing of cod spawning has been observed by other studies (e.g. Myers et al. 1993; Brander 1994), and has been linked to temperature and other regional differences.

The discrete spatial nature of Atlantic cod spawning in Trinity Bay is not unique and has been noted by many authors for other cod populations (e.g. Lawson and Rose 2000; Begg and Martiensdottir 2002; Lough et al. 2006; Bradbury et al. 2008). The persistence of the Smith Sound aggregation for more than 15 years (Rose 1996; DFO 2008) raises the question of how this stability is maintained and what is the source of new recruits. For Atlantic cod the regional differences in how temperature and spawning are linked has led to suggestions that spawning patterns might be tuned to local features such as optimal food conditions (Cushing 1990; Brander 1994), retention into specific nursery habitats (Bradbury et al. 2001, 2008; Miller et al 2006), or some combination of these factors (Sundby 2000).

Evidence presented here and elsewhere (Smedbol and Wrobleski 1997) suggests that spawning in Smith Sound is likely temperature driven, with peak spawning occurring when temperatures are warmest. Spawning in warmer waters and the associated reduction in development time results in shorter pelagic durations (Pepin et. al. 1997) and therefore generally shorter transport distances and likely increased local retention (Bradbury et al. 2001). This trend is generally validated with transport distance, estimated from COM calculations of Euclidian distances, and temperature. Specifically, the longest transport

distances estimated among all surveys corresponded with the coldest mean temperatures (Figure 2.13). As noted earlier, centre of mass calculations are particularly conservative and prone to bias, however, the centre of mass calculations agree with the trend of significantly more eggs on the western side of Trinity Bay and higher abundances of later stages further from Smith Sound (Figures 2.8-2.10). Although the inherent conservative nature of the center of mass calculations might diminish the utility of absolute measures of transport distance, the estimates nonetheless confirm observed trends in the field and predictions based on known relationships between temperatures, mortality and transport. These results indicate that the timing of Smith Sound spawning may favour a high level of retention. Presence of late eggs stages and larvae in and near Smith Sound are consistent with this hypothesis, suggesting that the majority of spawning activity occurs at times that decrease pelagic egg durations and therefore increase retention in and around Smith Sound.

Oceanographic conditions in Trinity Bay may also help to retain eggs and larvae near Smith Sound. Upwelling and other oceanographic features, such as gyres, have been shown to impact spatial patterns of pelagic propagules of species ranging from Chilean hake (Vargas and Castro 2001) to rockfishes (Bjorkstedt et al. 2002) to Atlantic cod (Munk et al. 1995; Munk 2007). Mean flow conditions in Trinity Bay are strongly influenced by an inshore, southerly flowing branch of the Labrador Current that enters the western side of Trinity Bay and exits on the eastern side (Yao 1986; Tittensor 2001,2002). There are two circulation features in Trinity Bay that are particularly relevant. A spatially and temporally consistent upwelling occurs north of Random Island

and at the mouth of Smith Sound (Schillinger et al. 2000; Tittensor et al. 2001,2002; Baumann et al. 2003; this study). A second feature is a cyclonic gyre that spans the width of the bay near the mouth of Smith Sound (Yao 1986; Tittensor et al. 2001,2002; Dalley et al. 2002; Figure 2.2). Dalley et al. (2002) suggested that the presence of oceanographic gyres likely lead to retention of larval capelin (*Mallotus villosus*) in Trinity Bay. The ichthyoplankton data here show a general association of all stages of eggs and larvae with the western side of Trinity Bay (Figures 2.8-2.11). The known development rates for eggs at ambient mixed-later temperatures in Trinity Bay from spawning to stage 4 would require at least 26-33 days (Pepin et al. 1997; Bradbury et al. 2001). Mean passive flow conditions estimated from flow modelling (Yao 1986; Baumann et al. 2003) and ADCP data (Tittensor 2001, 2002) could move eggs beyond the sampling spatial window in as few as 5 days, based on mean flow estimates of 10 $cm \bullet s^{-1}$ and Euclidian movement. Passive flow rates inferred from ichthyoplankon data of 0.32 $km \bullet day^{-1}$ for mixed-layer temperatures and 0.43 $km \bullet day^{-1}$ for surface temperatures represent less than 5% of estimated mean flow in Trinity Bay, further suggesting a strong role for the upwelling and gyre features. As with transport distance there are some issues with utilizing the centre of mass calculation, however, given that my estimates of centre of mass agree with spatial patterns of egg stage concentration I believe they offer some utility in describing transport. Even if the estimation of ~5% of expected flow rates is extremely conservative, the concurrent observation of spatial patterns does not suggest that dispersal is operating at the mean current rates estimating in the area. In addition, egg numbers were not consistently related to distance from Smith Sound, despite an expected decreases in number as a result of diffusion and cumulative mortality. Overall there is a high degree of

variance in the response of egg number to distance from Smith Sound, the expected source. This variability among surveys and survey seasons further negates a simple Euclidian dispersal interpretation. Furthermore, stage 1 eggs are consistently associated with the assumed natal source of Smith Sound, whereas stage 4 eggs are far more variable spatially among surveys. Collectively these results clearly suggest that some oceanographic feature influences egg dispersal trajectories and thus affects estimates of passive dispersal distances from ichthyoplankton spatial data. These results are also consistent with previous research in Trinity Bay that have found that oceanographic processes play a significant role in the spatial pattern of ichthyoplankton (Dalley et al. 2002).

Given the constraints that the physical environment imparts on dispersal (i.e. circulation and seasonal temperatures), timing of spawning in the context of circulation, development, and spawning strategy is vital in order to place eggs in a suitable environment (Gawarkiewicz et al. 2007; Snelgrove et al. 2008). Evidence from ichthyoplankton data in Smith Sound and Trinity Bay suggests that a combination of spawning strategy and oceanographic processes might result in a highly retentive system. Success of a spawning strategy is usually constrained by the placement of passive propagules into water masses that have favourable food conditions (Cushing 1990). The observation of significantly higher primary productivity, as indicated by fluorescence, and zooplankton abundance on the western coast of Trinity Bay suggest that this region of bay provides a favourable feeding environment, possibly leading to higher survival and recruitment to juvenile stages.

The protracted nature of cod spawning and the expected seasonal changes in environmental conditions lead to the prediction that seasonal variation in spawning will influence recruitment success (Bradbury et al. 2001). Previous work on the relationship between spawning strategy and environmental variation suggests that recruitment might be largely environmentally driven and that seasonal-spatial variation in recruitment patterns might therefore be expected. Temperature has been shown to play a pivotal role in pelagic egg mortality exhibiting both negative (Dahlberg 1979) and positive (Houde 1989; Pepin 1991) correlations depending on what process is driving the mortality measured. In particular, spawning in colder temperatures is expected to extend pelagic durations and result in prolonged exposure to high mortality rates that characterize pelagic egg stages (Dahlberg 1979) and possible flushing from inshore nursery areas (Bradbury et al. 2001; Dalley et al. 2002). Data presented in this study suggest otherwise. Spatial patterns of egg stages suggest limited dispersal, with a mean transport of only 0.43 km•day^{-1} (s.d. = 0.25). The ratio of peak stage 1 to stage 4 egg abundances does not vary seasonally despite approximately a 1 week longer in development times (based on mean mixed layer temperatures), indicating that survival of the egg stage likely does not vary significantly among seasons. The absence of seasonal variation in spatial patterns suggests that oceanographic processes that facilitate retention persist through the spawning period.

Smith Sound the source

The data presented here suggests that Smith Sound represents the major source of CHW eggs in the Trinity Bay system. The highest abundance of stage 1 CHW eggs is consistently associated with the western side of Trinity Bay near the mouth of Smith Sound from spring through summer and from one year to the next (Figures 2.8-2.10). Only during one survey in mid-July 2004 was there any suggestion of significant movement towards the mouth of Trinity Bay. Given that the Smith Sound stock has been acknowledged as the largest remaining spawning biomass in the 2J3KL complex (DFO 2008), detecting any outside recruitment input would be difficult, because any signal would be drowned relative to output from Smith Sound. Focussing on spatial distributions alone, spatial analysis clearly illustrates the importance of the Smith Sound spawning aggregation on the Trinity Bay system, but suggests, at least anecdotally, that the movement of early life history stages to the broader 2J3KL system is small relative to the retention within.

Despite a long time series of acoustic estimates of cod biomass from 1995 to the present (Rose 1996; Rose 2003; DFO 2000-2008), and numerous studies on behaviour and physiology of spawning cod from the area (e.g. Wroblewski et al. 1994; Rideout and Rose 2006), there have been few estimates of source-sink dynamics in Trinity Bay (Smedbol and Wroblewski 1997). One key piece of information to this question is the estimate of egg loss from Smith Sound to the larger Trinity Bay system.

My model simulations estimated that daily net mortality in Smith Sound was approximately 27%. This mortality rate is similar to the 28% daily net mortality rates

estimated by Panteleev et al. (2008) for silver hake (*Merluccius bininearis*) on the Scotian Shelf in a similar numerical simulation of egg and larval dispersal from a geographic location. Daily net mortality is the sum of natural mortality and mortality resulting from advective loss from the system. Model simulations that incorporate data variability suggest that daily loss from the Smith Sound system is between 2-15% with a mean of 13% for 2004 and ~9% for all surveys combined. These results also demonstrate a positive association with estimated survey loss rates and day of year. The seasonal variation in estimated loss rates might reflect differences in spawning output during the protracted spawning season. A four-fold increase in spawning (estimated from Smith Sound surveys) in July within a two to three week period would result in spike in the relative frequency of stage 1 eggs and drive the seasonal model of loss rates. Trinity Bay ichthyoplankton data demonstrates an increase in the relative frequency of stage 1 eggs near the July spawning peak relative to May surveys, as would be predicted from the model estimates of loss. The 13% daily loss estimate from 2004 is likely the best measure because it incorporates seasonal differences in spawning and temperature.

Another approach to interpreting the loss rates from Smith Sound is to reverse the equation and estimate natural mortality loss from Smith Sound. Estimates of mortality derived from empirical data indicate natural mortality is between 0.06 to 0.08/day. This range is slightly lower than previous estimates of natural mortality, which range between 0.1/day to 0.3/day (Campana et al. 1989; Sundby et al. 1989; Heath 1992; Bradbury et al. 2001; Panteleev et al. 2004; Mountain et al. 2008). Pepin et al. (1995) demonstrated that physical forcing confounds estimates of mortality and this effect is scale dependent. To

account for this Pepin et al. (1995) suggest a correction factor or $Area^{-1/2}$ be applied. Given that physical forcing often drives spatial patterns in ichthyplankton (Dalley et al. 2002; this study) a correction factor seemed appropriate in this case. With the correction factor accounting for the influence of local physical forcing on the estimates of morality (Pepin et al. 1995), the estimates of 0.09/day (all years) and 0.13/day (2004 only) are within the range of published daily mortality rates. These results again reiterate that oceanographic features have a strong influence on distributions of eggs near the mouth of Smith Sound.

The predictive value of the loss estimate from Smith Sound was improved (~ 6% of the variance) with the inclusion of a multiplication factor for individual stage mortality. This dependency on differences in egg stage mortality, albeit weak, might be a product of vertical mixing in Smith Sound. An underlying assumption in this model is that spawning is uniform throughout the Sound and that eggs are completely mixed. Because the probability of an egg leaving Smith Sound increases as a function of ontogenetic development, the assumption of uniform spawning and mixing is reasonable; the longer the duration of each egg stage in the system, the more likely an individual egg is to be advected from the system. This result provides support for the suitability of the model in estimating spawning pattern and mortality.

Summary

The data and model simulations presented here suggest that timing of spawning acts in concert with oceanographic features to retain larvae near or within Smith Sound where

food conditions are generally favourable. Contrary to studies in other systems (Bradbury et al. 2001), there is little evidence for seasonal differences in the retention of reproductive propagules. The results from analysis of spatio-temporal patterns of early life history stages of Atlantic cod suggest that connectivity potential from spawning events in Smith Sound decreases as a function of distance from Smith Sound. Daily loss rates from Smith Sound are predicted to range between 8-13% daily. Given the highly retentive nature of the Trinity Bay-Smith Sound system, the density-dependent emigration theory, proposed by Rose (1996), could still be applied but only when recruitment success triggers density dependent movement of spawners from Trinity Bay. There is some evidence that adults in spawning condition do move from Smith Sound into Trinity Bay and beyond (C. Morris, personnel communication, Department of Fisheries and Oceans, North-west Atlantic Fisheries Centre, St. John's, NL, A1C 5X1 Canada), but the contribution this could provide to connectivity is unknown. The potential for inshore spawners to contribute significantly to the recovery of offshore stocks (Hutchings and Myers 1994; Rose 1996) may only really come to fruition if density dependent inshore-offshore spillover occurs among adults. Evidence from my study suggests that connectivity during the early life history of Atlantic cod is limited in this system and likely plays a significant structuring role only on smaller (bay-sized) spatial scales.

The effects of wind forcing and circulation could not be directly measured because of data limitations, however, the parameters and observations presented in this study are consistent with and build on existing data on dispersal and connectivity in Trinity Bay.

This study illustrates processes that regulate dispersal from one of the largest remaining pawning aggregations from the diminished 2J3KL cod stock complex.

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Table 2.1 Key for identifying taxonomic stages of cod-haddock-witch flounder (CHW) eggs according to methods outlined in (Markle and Frost 1985).

Stage	Description
I	From fertilization until formation of embryonic axis
II	From end of stage one until embryo pigmentation begins
III	From stage two until embryo wraps completely around yolk sac and defined pigment patterns are present
IV	From Stage three until hatch

Table 2.2 Results for General Linear Model Analysis of Variance comparing physical and biological parameters between sides Trinity Bay (Fluorescence) and between survey average and upwelling (stations within 7km of Bonaventure Head).

Variable	Factor	df	*F*-value	p-value
Fluorescence	Side of bay	1	10.420	0.002
	Survey	6	3.957	0.001
	Interaction	6	3.699	0.002
Mixed Layer Temperature	Bonaventure Head	1	12.166	0.001
	Survey	6	32.927	<0.0001
	Interaction	6	0.322	0.925
Zooplankton*	Bonaventure Head	1	6.901	0.013
	Survey	6	8.866	0.005
	Interaction	6	0.694	0.410

* zooplankton data only available for 2006 surveys

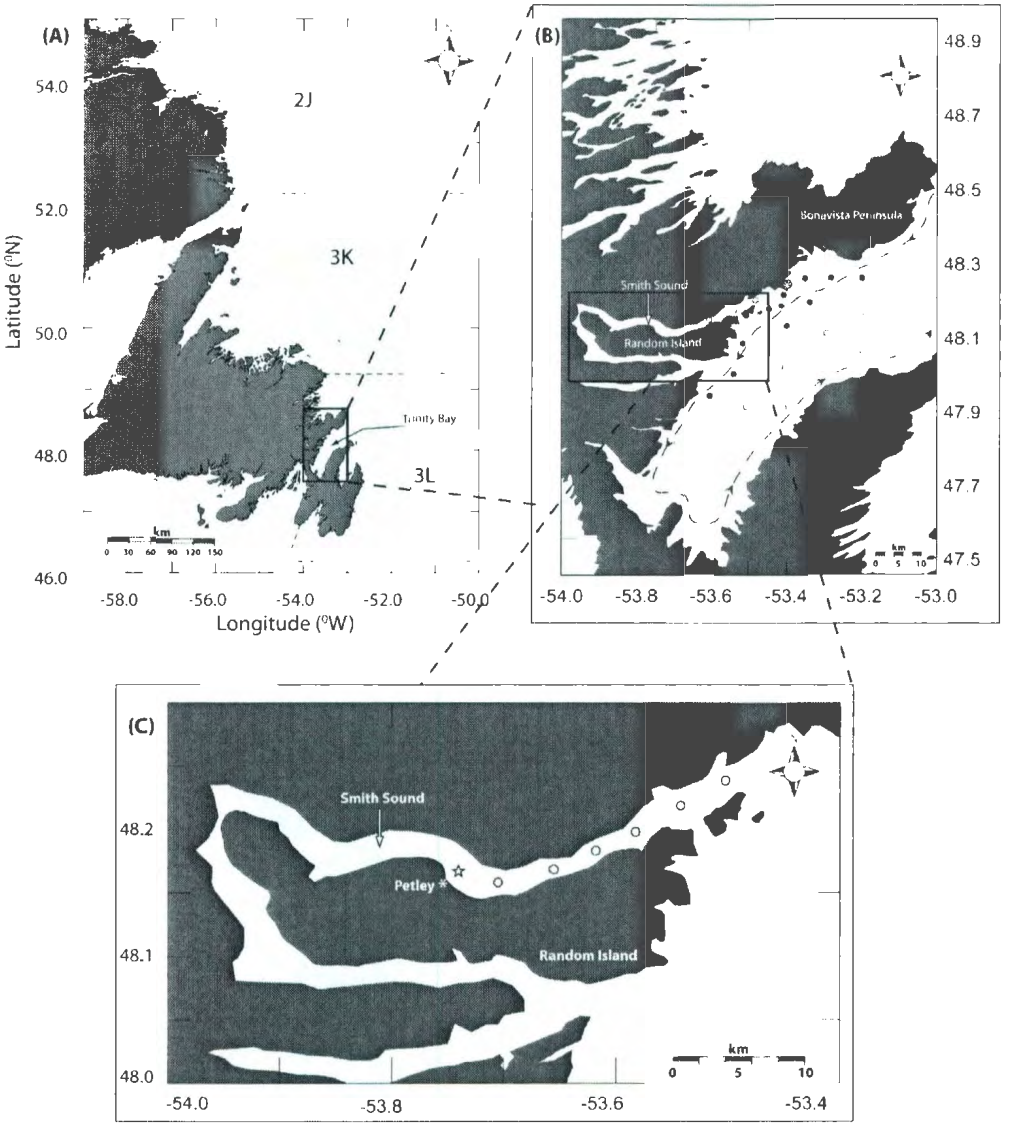

Figure 2.1(a) Location of NAFO divisions 2J3KL in the northwest Atlantic Ocean. **(b)** Trinity Bay ichthyoplankton survey array sampled in May 2004/2006 and July 2004. Black circles represent eastern Trinity Bay Stations, dashed line represents mean passive flow conditons (Tittensor 2001;2002), and * represents Bonaventure Head. **(c)** Map of Smith Sound, Trinity Bay, showing ring net survey stations (open circles) sampled March to June 2006 and March to August 2007. Star symbol refers to temperature logger mooring location near Petley, Newfoundland.

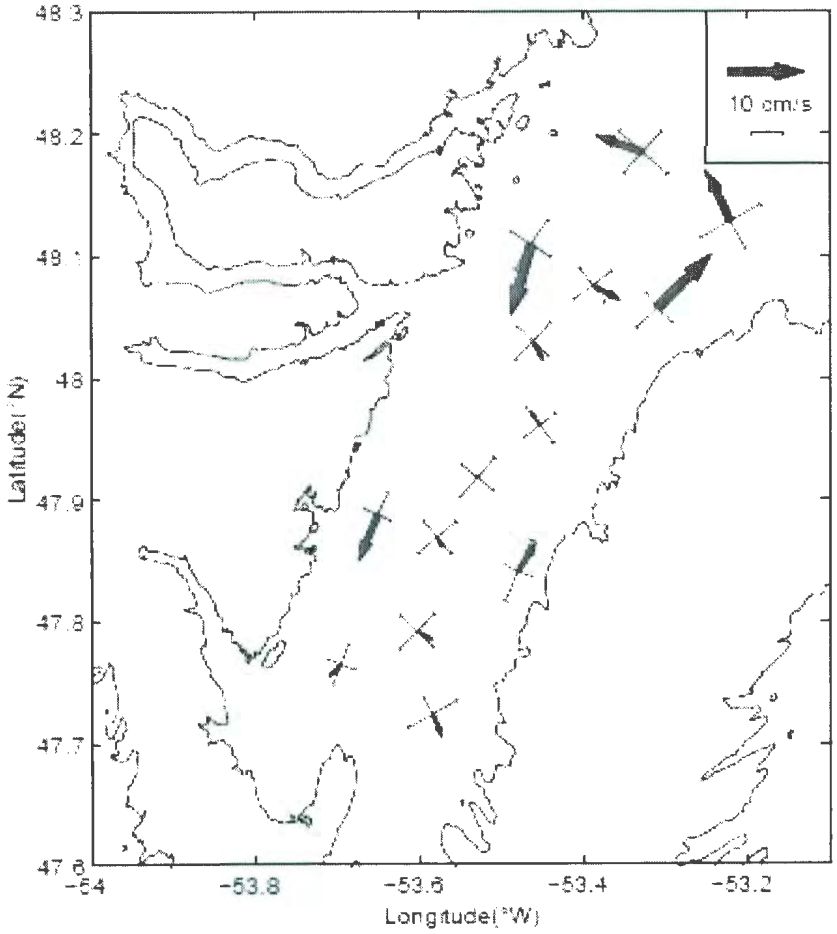

Figure 2.2 Exert from Tittensor et al. 2002*. Mean currents, Trinity Bay, May – August 2002, at a depth of 20m. The solid axes represent standard deviation of the flow along the direction of maximum and minimum variance. *Reproduced with permission of author.

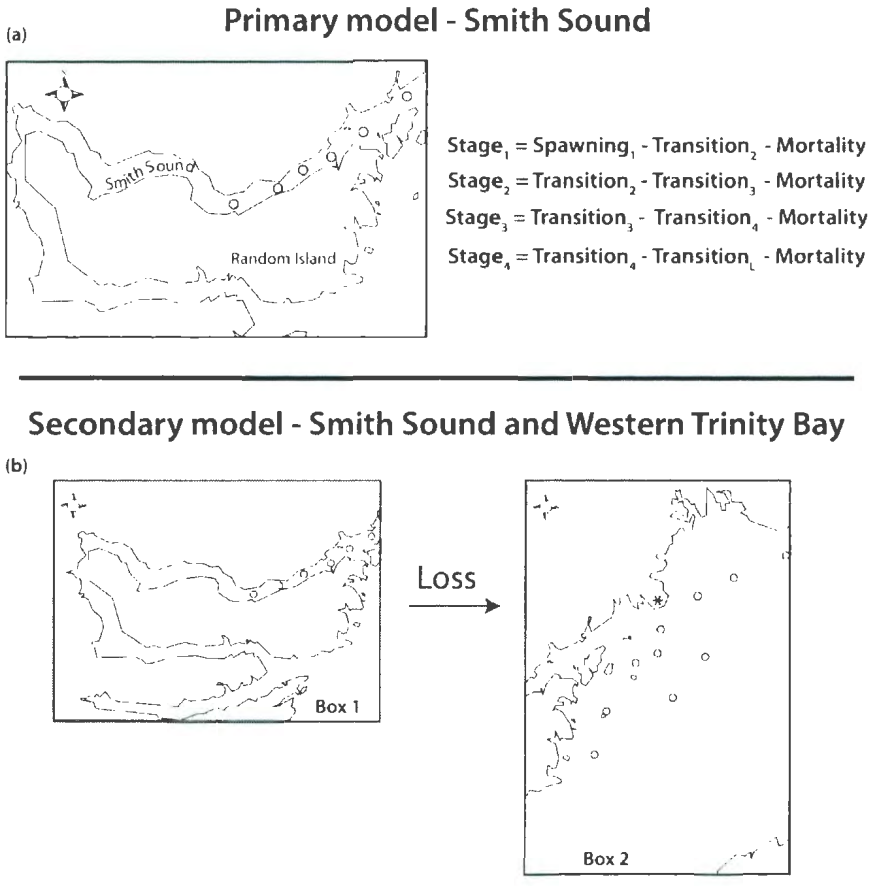

Figure 2.3 Illustration of model setup for primary (**a**) and secondary (**b**) models. Equations define how the number of eggs in Smith Sound was determined in the model during daily time steps. Source terms secondary model (**b**) Box 2 are loss terms from Box 1 derived as a component of the daily mortality term. "o" symbols refer to sample stations. "*" refers to Bonaventure Head.

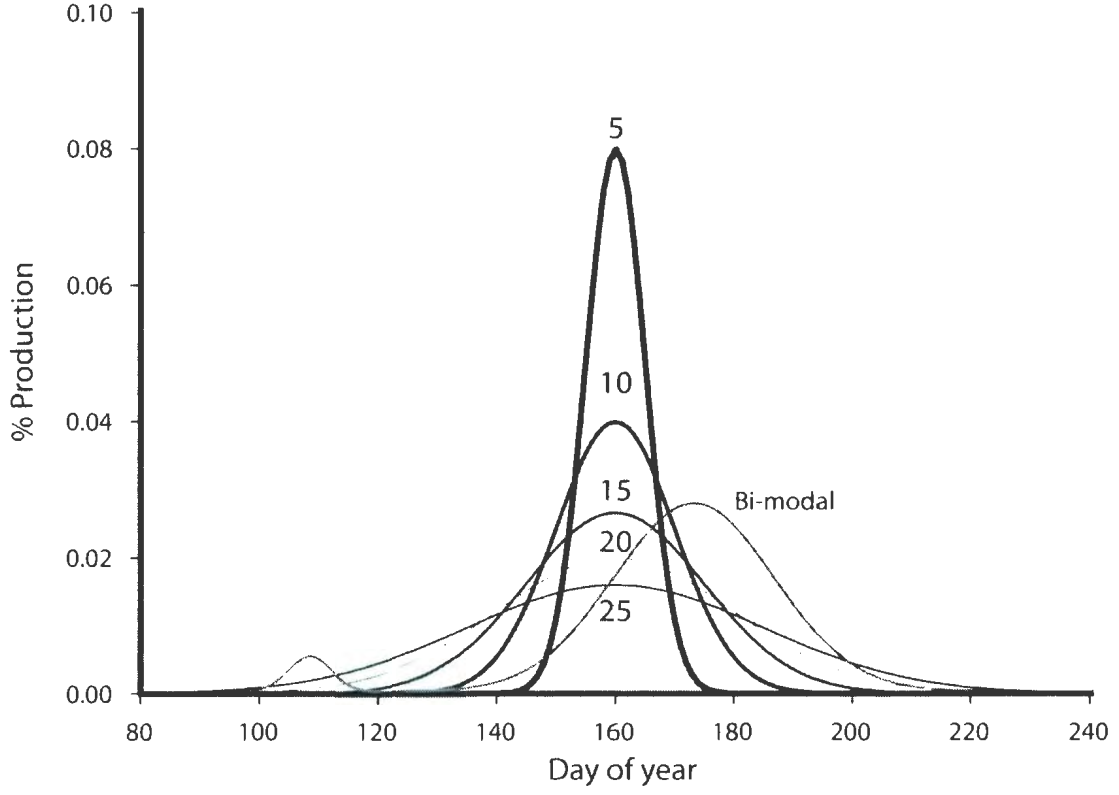

Figure 2.4 Temporal spawning treatments: Bi-modal treatment derived from survey data and Gaussian curves derived with varying degrees of protraction (denoted by numerals 5-25).

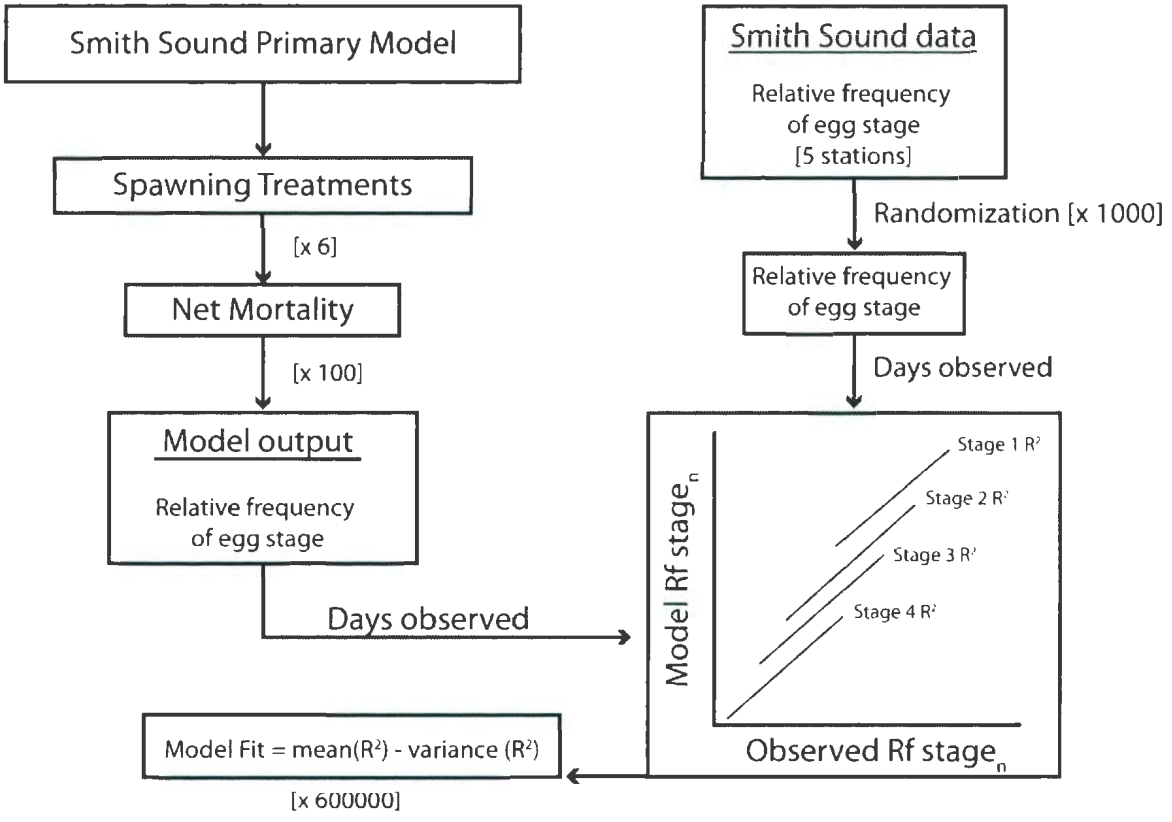

Figure 2.5 Flow diagram detailing how the primary model estimates both spawning scenario and net mortality in Smith Sound. r^2 is the coefficient of determination and Rf is the relative frequency of a particular egg stage.

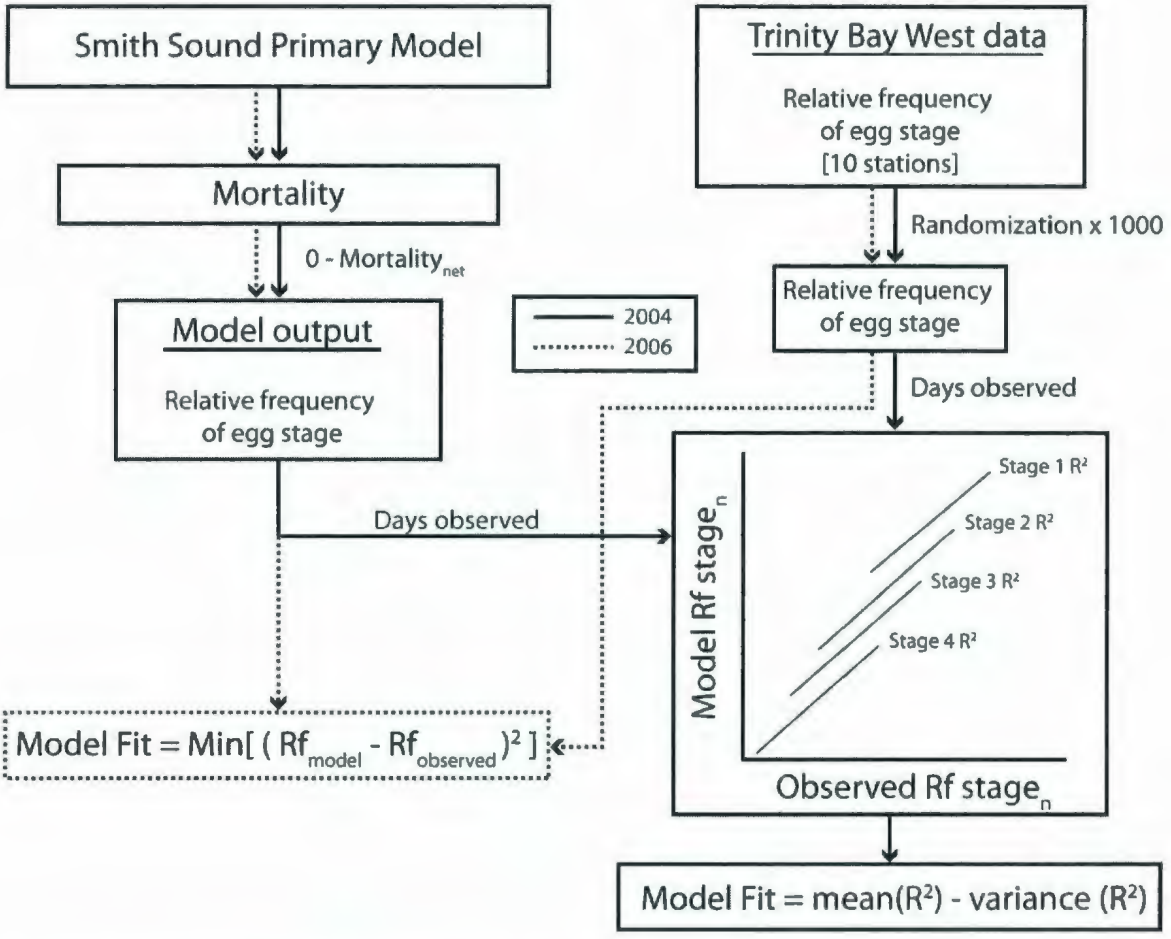

Figure 2.6 Flow diagram detailing how the primary and secondary models were integrated to estimate a mean daily loss from Smith Sound. r^2 is the coefficient of determination and Rf is the relative frequency of a particular egg stage.

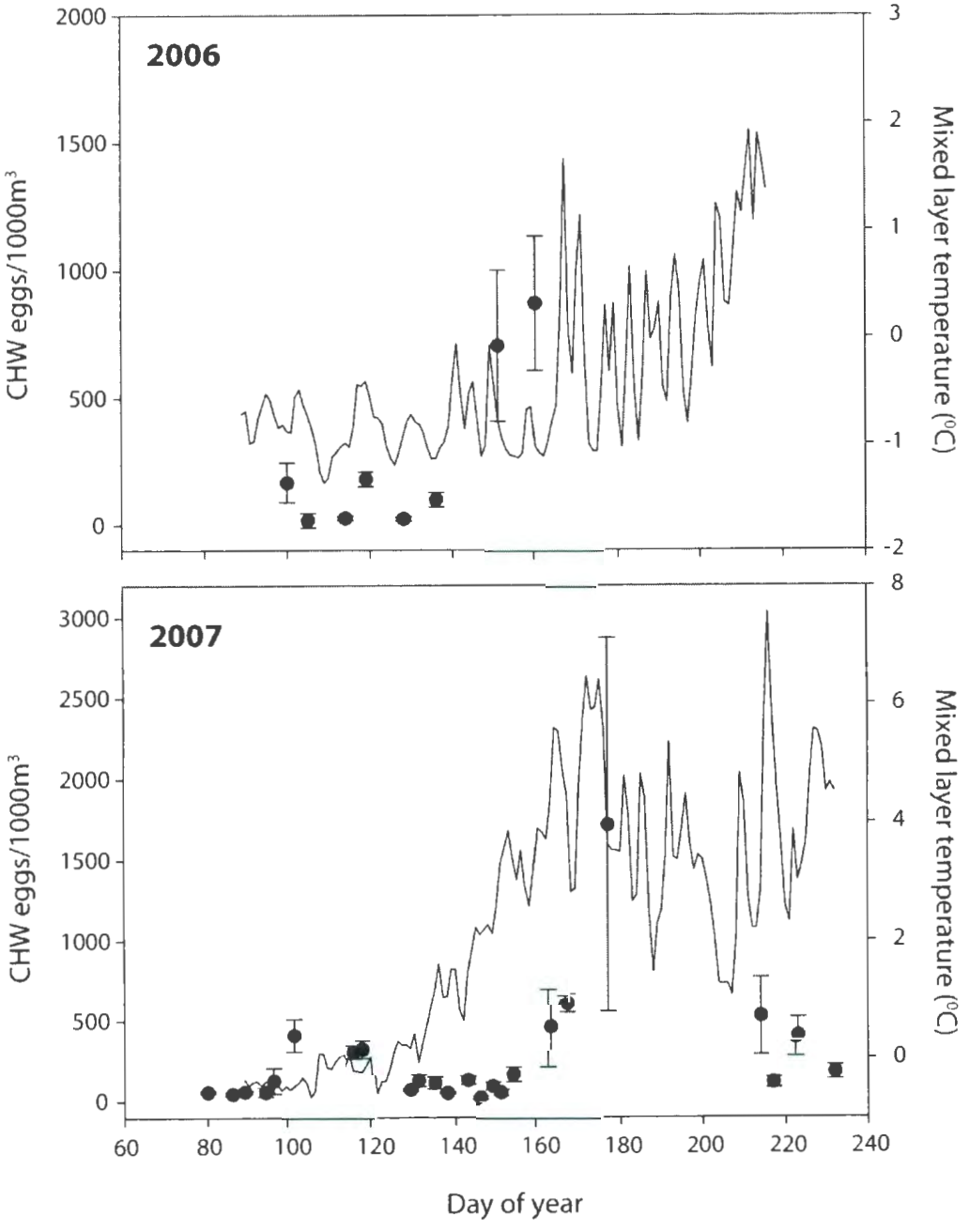

Figure 2.7 Mean stage 1 CHW egg density ± standard error sampled in Smith Sound during 2006-2007 ring net surveys. Solid line indicates mean mixed-layer temperature (<40 m).

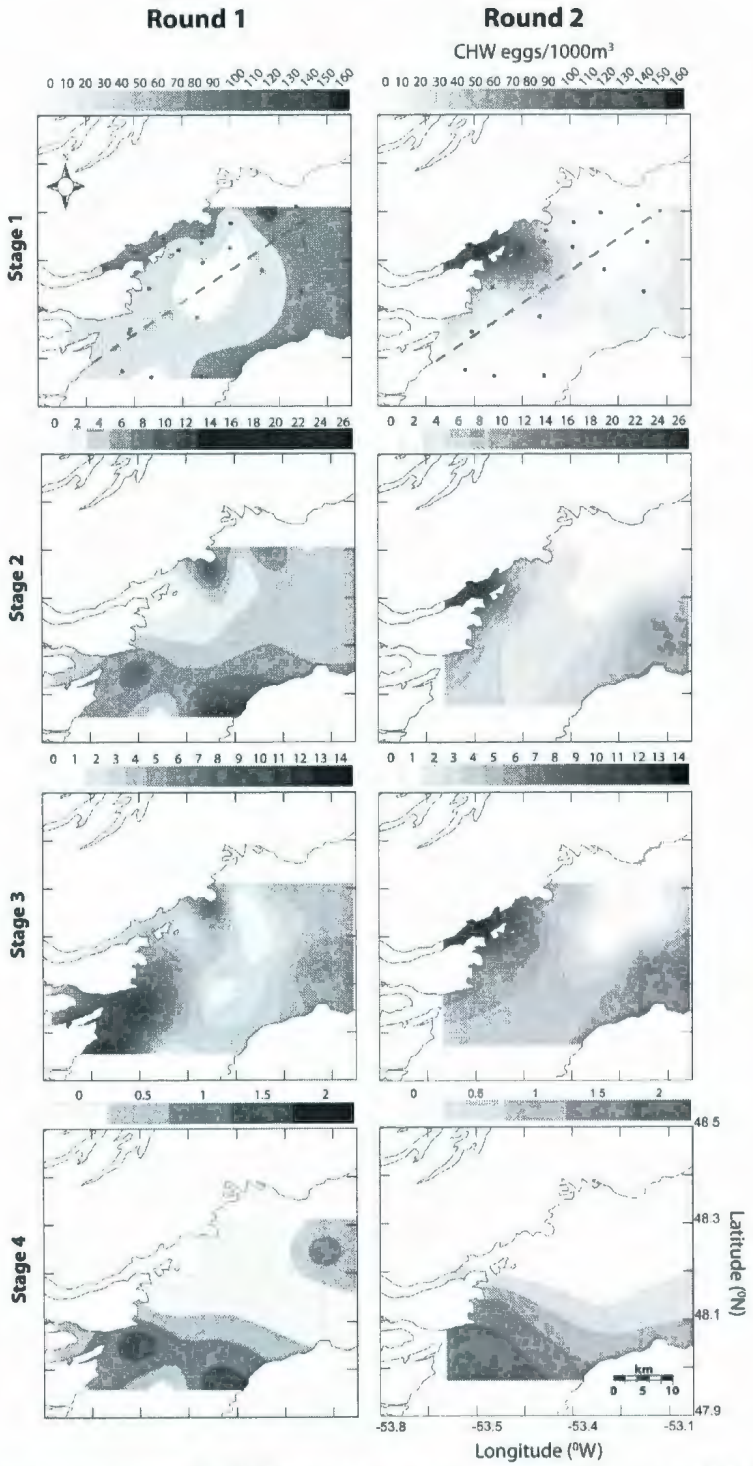

Figure 2.8 Spatially-contoured CHW eggs stage abundance for May 2004 Trinity Bay Tucker trawl surveys. Dots represent sample station array and dashed line represents east west divide for bay scale comparisons.

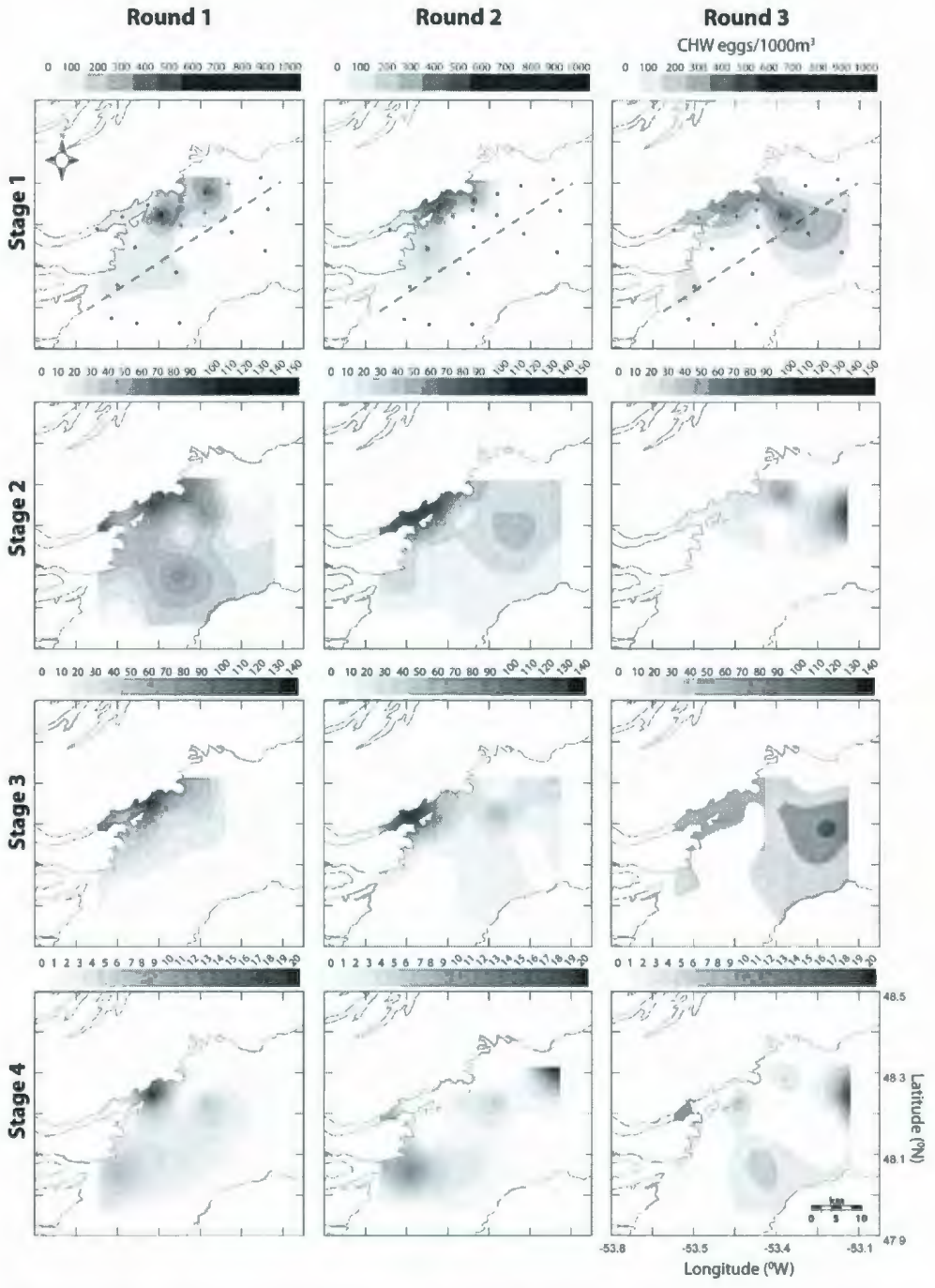

Figure 2.9 Spatially-contoured CHW egg stage abundances for July 2004 Trinity Bay Tucker trawl surveys. Dots represent sample station array and dashed line represents east-west divide for bay-scale comparisons.

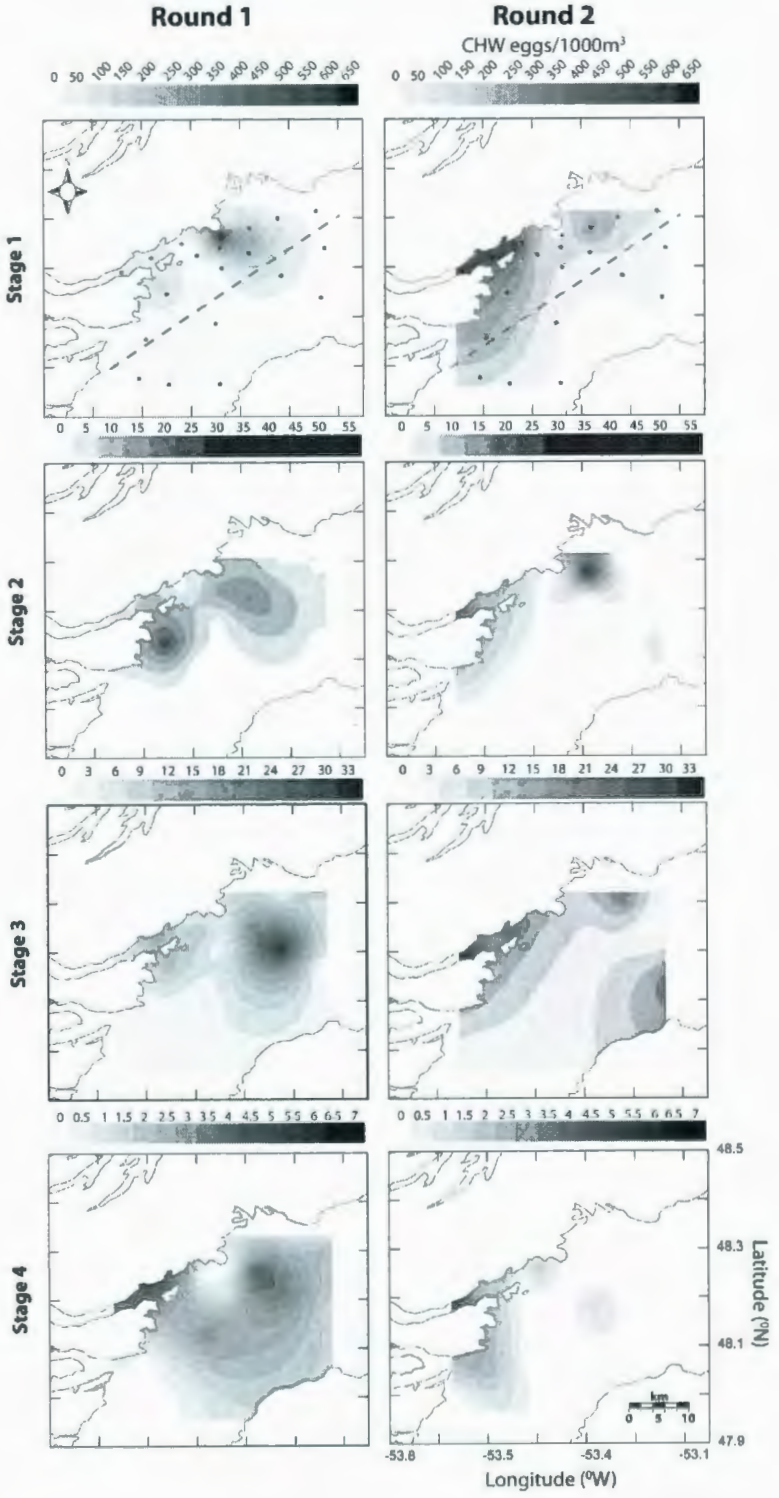

Figure 2.10 Spatially contoured CHW egg stage abundances for May 2006 Tucker trawl surveys. Dots represent sample station array and dashed line represents east-west divide for bay-scale comparisons.

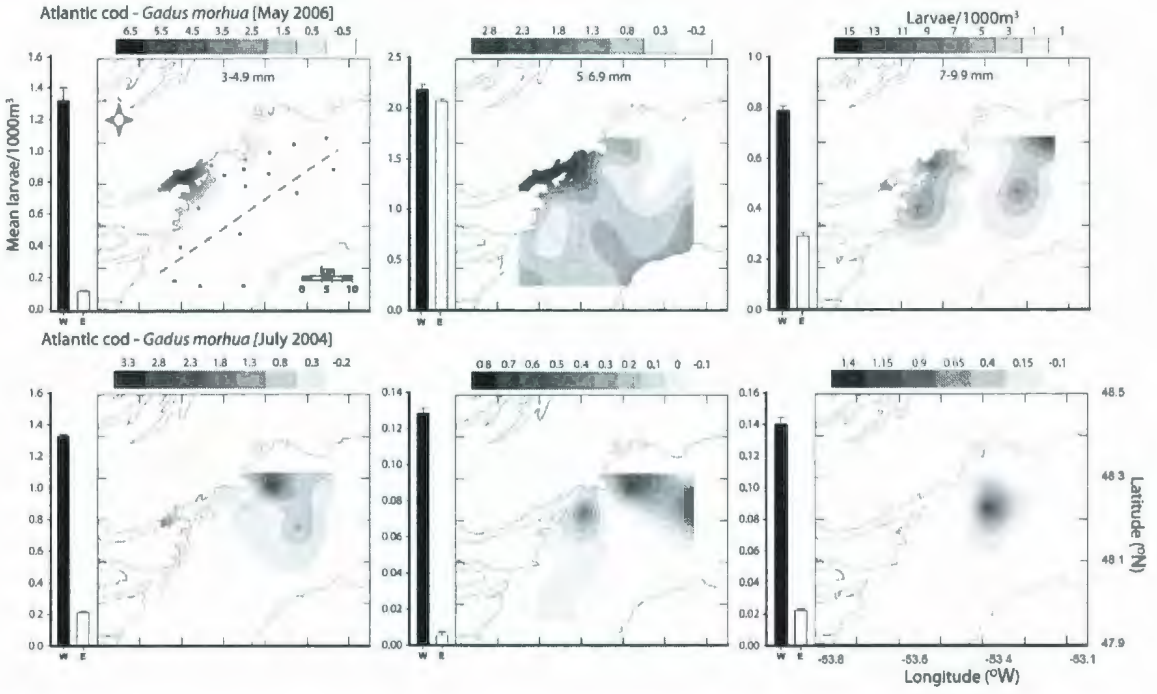

Figure 2.11 Spatially-contoured species size abundance binned into early, middle, and late larval development sizes. Side bars represent mean larval abundance for western (W, black bar) and eastern (W, white bar) regions of Trinity Bay. Dashed line represents the boundary between the sample regions and dots represent sample stations.

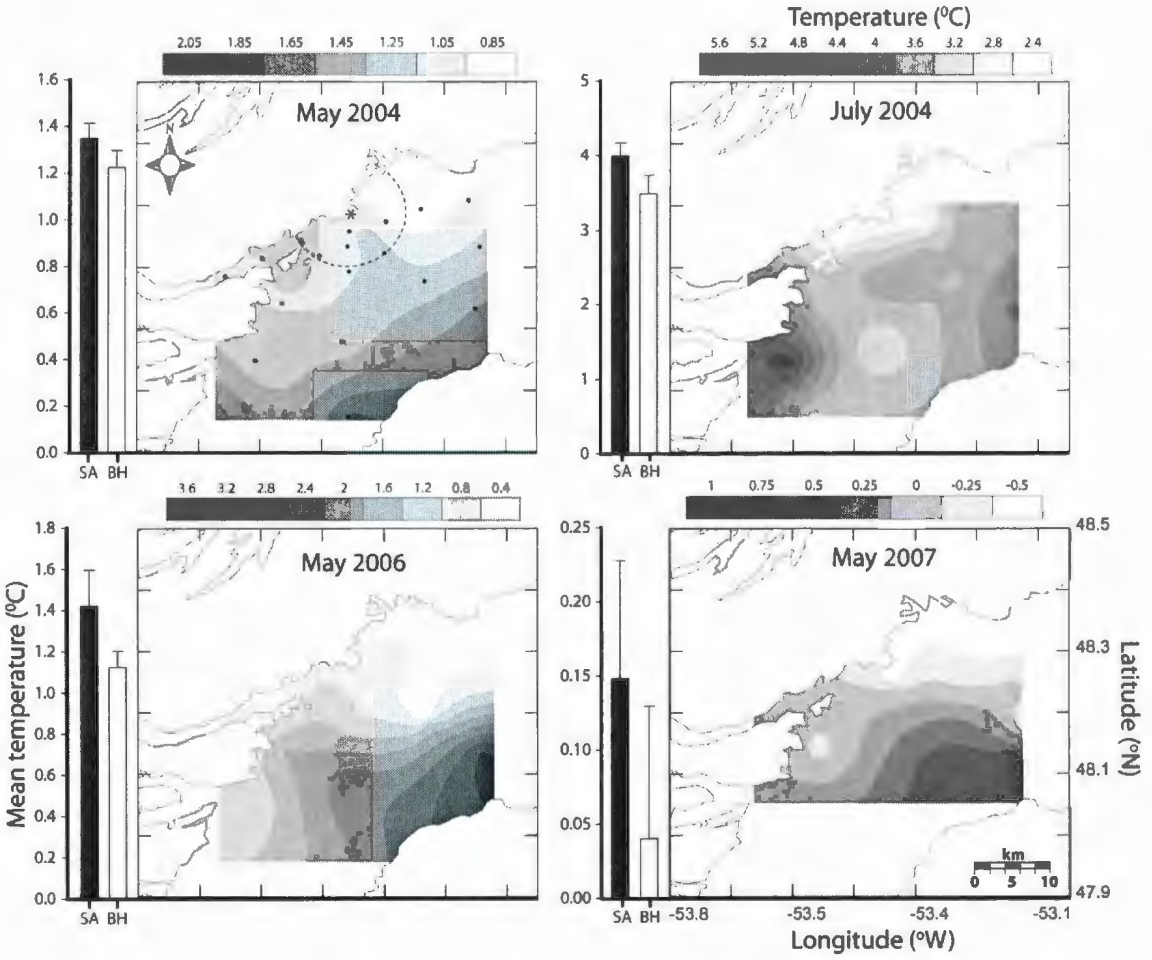

Figure 2.12 Spatially-contoured CTD cast temperature data for the mixed-layer (average up to 40 m depth) collected during ichthyoplankton surveys of Trinity Bay 2004-2007. Barplots represent mean temperatures ± standard error for the survey average (SA, black bar) and data from within 7 km of Bonaventure Head (BH, white bar). Dashed line represents the radius of data sampled for Bonaventure Head (*) temperature calculations and dots represent station array used for all surveys.

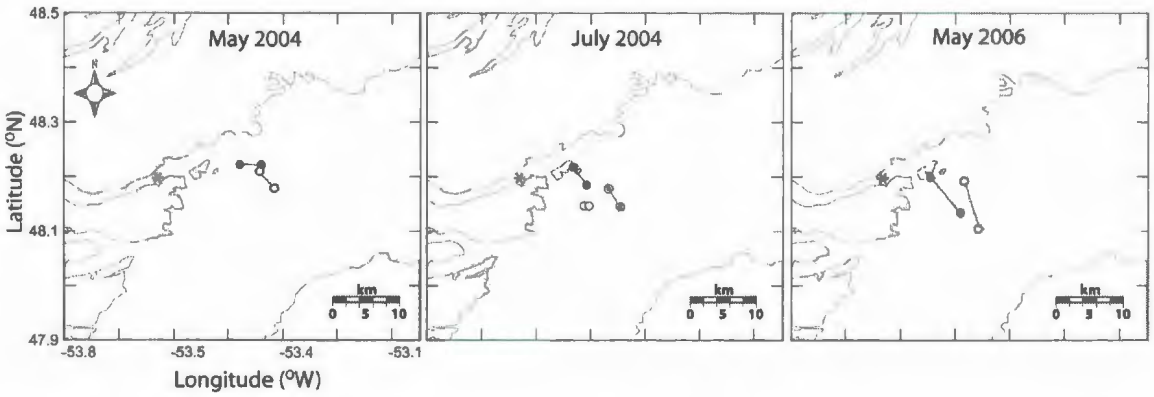

Figure 2.13 Centre of mass calculations for early (stages 1-2) and late (stages 3-4) CHW egg stages. Early stages in all cases are the closest Smith Sound (*). Solid circles refer to round 1, open circles refer to round 2, open circles with inner solid circles indicate round 3 centre of mass calculations.

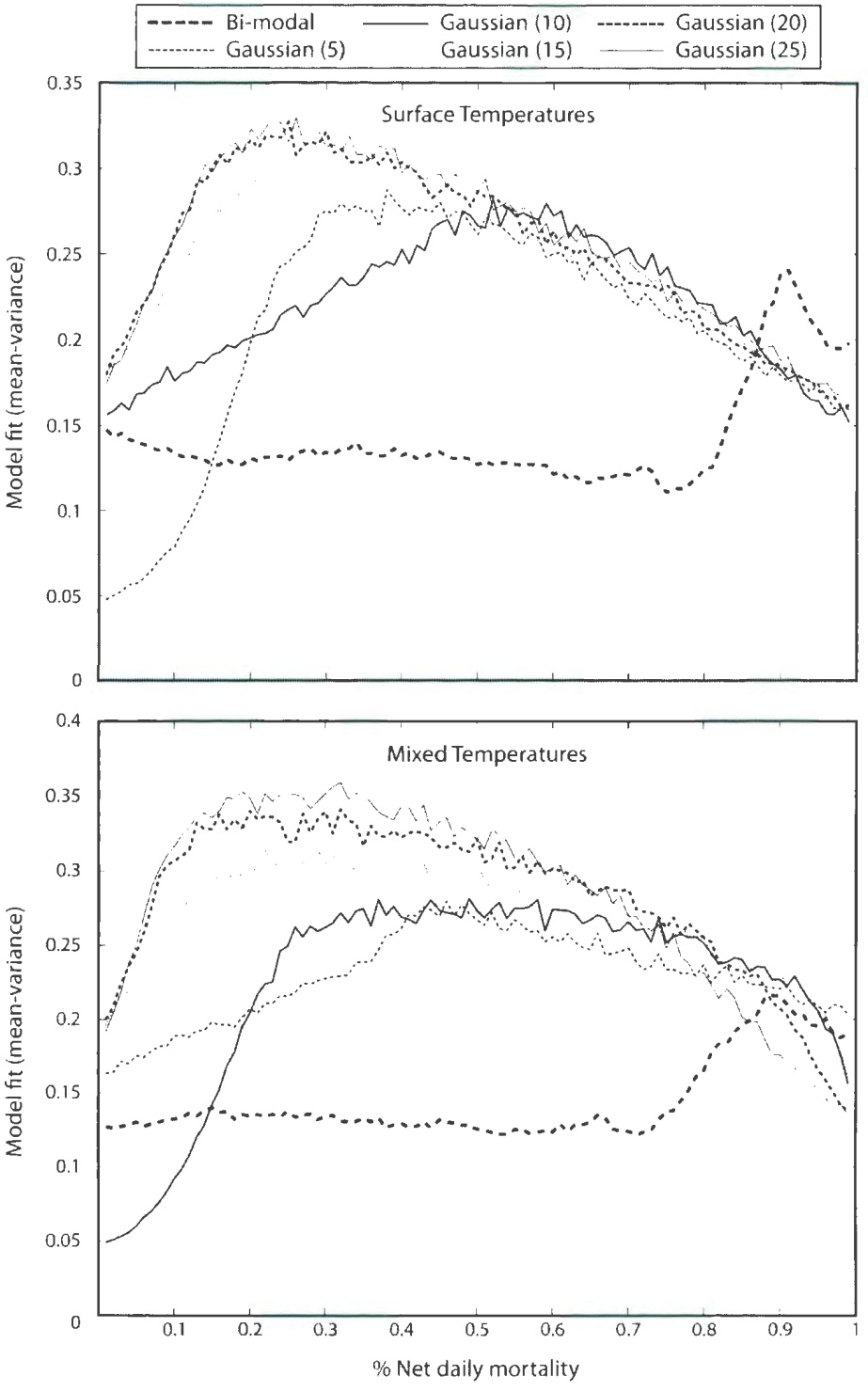

Figure 2.14 Model fit results for varying spawning scenarios, temperatures and estimated daily net mortality. Data presented is the overall mean of the model fits produced in 1000 randomizations of Smith Sound data.

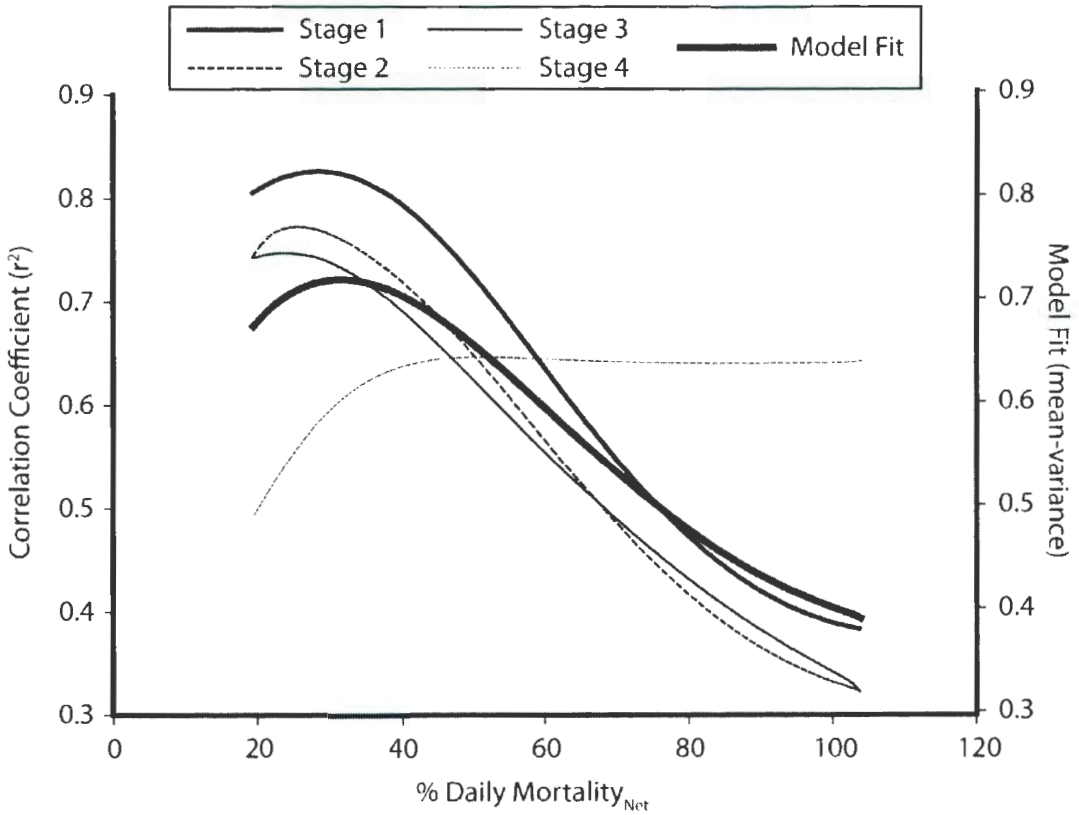

Figure 2.15 Model results for explained variance (r^2) for each egg stage with varying net mortality. Also plotted is the overall model fit maximizing mean r^2 and minimizing the variance among stage r^2 values.

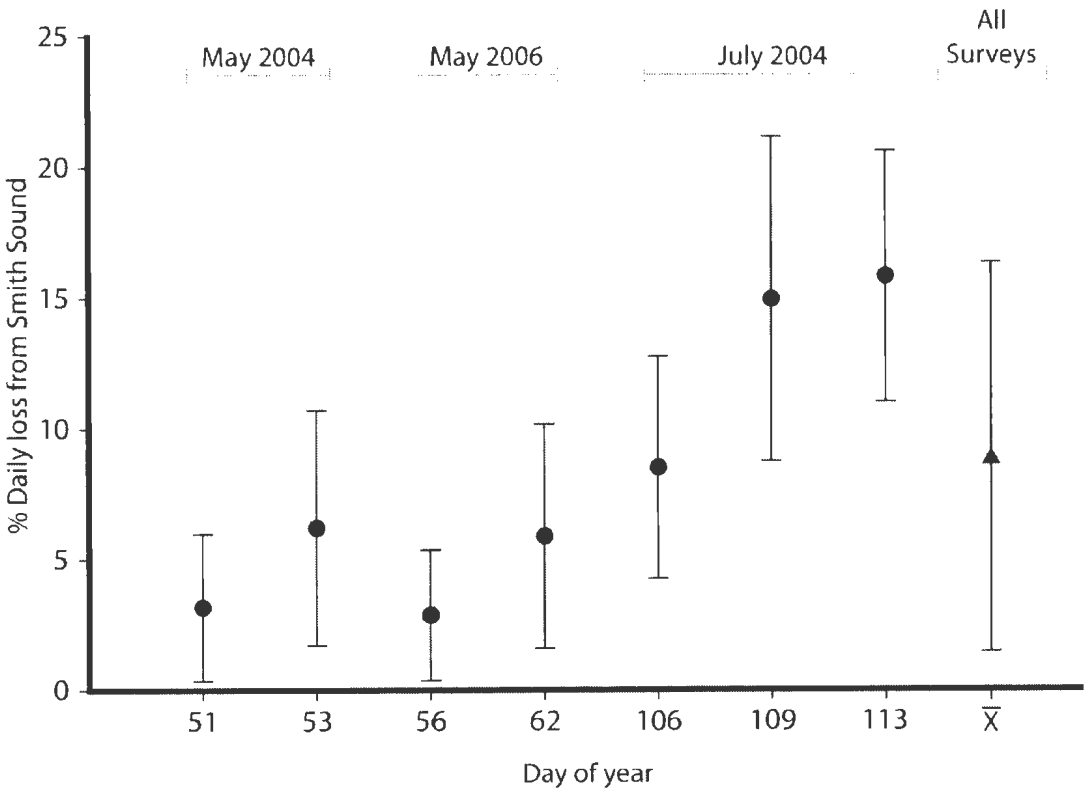

Figure 2.16 Estimates of percent daily advection of CHW eggs from Smith Sound (± 1 S.d.). Error bars are estimated from 1000 randomizations of western Trinity Bay survey data.

Chapter 3. Connectivity during the early life history of coastal Newfoundland fishes: Does active behaviour play a role?

3.1 Introduction

Many marine organisms have eggs and larvae that are transported during a pelagic dispersive stage, through an interaction between passive oceanographic processes (e.g., Karasiova and Zezera 2005; Bradbury et al. 2003) and active behaviour (e.g., Leis et al. 1996). In spatially structured marine populations the degree of dispersal among local populations is defined as connectivity. These connective processes are essential to the maintenance of spatial structure (Bode et al. 2006) and the stability of marine populations (Hastings and Botsford 2003). The success of the dispersal phase is rooted in the placement of propagules into suitable nursery habitat, greatly increasing probability of survival. Elucidation of the passive and active contributions to larval dispersal has been of particular interest to marine ecologists and fisheries biologists for the past century (Harden-Jones 1968; Bradbury and Snelgrove 2001). Passive contributions have been addressed using a variety of techniques including direct observation with passive drifters (Panteleev et al. 2004) or neutrally buoyant particles (Taggart et al. 2006), and numerically models of drift based on circulation data (Davidson and deYoung 1995). These techniques have led to models that simulate drift at relatively fine spatial scales (Laprise and Pepin 1995).

The swimming ability of larvae has been hypothesized to be a critical factor in the success or failure of the dispersal phase (Fisher and Bellwood 2002). Laboratory studies

represent a useful approach to illustrate the possible contributions of swimming to spatial and temporal patterns observed in the field. Laboratory observations on the swimming reef fish have suggested that larvae have a diverse range of swimming and behavioural capabilities (Stobutzki and Bellwood 1997; Leis 2007a,b). Much of this work has focused on larvae of coral reef fish. However, recent laboratory swimming experiments by Guan et al. (2008) demonstrated similar, though weaker, swimming capabilities in several cold ocean species including Atlantic cod (*Gadus morhua*). Data from these studies, both from warm and cold ocean systems, suggest that larvae have the potential to mediate their own spatial distributions through active behaviour over vertical and horizontal scales, potentially enhancing their capacity to select suitable habitat that can be vitally important to recruitment.

Any definitive demonstration of whether swimming influences spatial structure in the field is difficult without direct observation. Studies of coral reef systems (Leis et al. 2007a,b) have included direct observations of larvae in the field and have determined that swimming behaviour actively mediates spatial distributions. In cold ocean systems, this type of observation is much more difficult because visibility is often limited and larval concentrations are typically very low. Studies by Bradbury et al. (2003) and Methven et al. (2003) have elucidated aspects of swimming ability through interpretations of observed field spatial patterns. Spatial distributions of marine organisms are rarely uniform and are often patchy. The causes of patchy spatial distributions of fish larvae are numerous and include passive oceanographic mechanisms (Karasiova 2005; Stabeno et al. 1996), predation (Hewitt 1981), and active behaviour by the organism (McGurk 1987;

Mattsurra and Hewitt 1995). The observation that patchiness changes from highly patchy to dispersed to highly patchy as a function of larval size, in a roughly consistent "*U*" shaped pattern (Bradbury et al. 2003), suggests that passive processes alone cannot explain spatial distribution. Swimming capacity in larvae increases as they grow larger (Williams et al. 1996; Guan et al. 2008). Therefore, it has been argued, through analysis ontogentic changes in spatial structure, that active behaviour could drive at least some aspects of the spatial heterogeneity observed in marine systems (Hewitt 1981; Mattsura and Hewitt 1995; Stabeno et al. 1996; Methven et al. 2003)

One component not addressed in these patchiness studies is the role of the hydrodynamic environment and how it might provide another framework on which to present swimming as a calculable influence on spatial heterogeneity during the larval period. Many papers have applied the concepts of functional morphology to swimming and the hydrodynamic environment (e.g. Webb 1984; Webb and Weihs 1986; Muller and Videler 1996). Functional morphology addresses the relationship between structure, function, and the mechanical principles that define the interaction (Webb and Weihs 1986). Allometric analysis provides a framework to assess functional relationships by illustrating how an organism changes shape as it grows. By comparing the relative growth of parts of an organism to an overall growth index, it is possible to determine how the geometry of an organism changes through ontogeny, which in turn has a direct relationship to function. The physical environment around the organism defines the efficiency of structure to its function, especially in small swimming organisms (Webb and Weihs 1986). The ratio of viscous (decreases swimming efficiency) to inertial (increases swimming efficiency)

forces defines the hydrodynamic environment around an organism. Small, slow-moving larvae typically exist in an environment where viscous drag dominates and swimming is inefficient relative to larger, faster larvae in the inertial hydrodynamic environment (Fuiman and Batty 1997; Hunt vonHerbing 2002). Many pelagic larvae hatch at small sizes, and the majority of their pelagic duration is therefore considered passive (Davidson and deYoung 1995). The onset of detectable swimming ability should occur where larvae make the transition from a flow environment where is swimming is inefficient to one more conducive to swimming. In addition to reducing or enhancing swimming ability, the hydrodynamic environment has been shown to influence growth patterns (Muller and Videler 1996). For example, larvae which grow faster along the longitudinal axis (i.e., length) escape the viscosity often experienced by newly hatched larvae at an earlier age than larvae that grow longer more slowly. Larval morphology is intrinsically linked to locomotion, especially in fluid environments where the morphology of the organism can have profound ramifications for the interaction with the fluid environment (Fuiman and Batty 1997). The examination of morphological and allometric growth relationships within a hydromechanical perspective can lead to insights on how the hydrodynamic environment influences growth (McHenry and Lauder 2006).

Recent studies in coastal Newfoundland suggest that swimming plays a significant role in dispersal and thus connectivity (Bradbury et al. 2003). The critical analysis of the spatial structure and environmental conditions provided by Bradbury et al. (2003), adds additional evidence that larval swimming plays a role in dispersal processes in coastal Newfoundland. It also answers questions posed by Leis (2007 a) regarding the differences

in onset of swimming ability in cold ocean species and how this might be intuitively linked to the hydrodynamic swimming environment experienced by larvae. My study builds upon the argument presented by Bradbury et al. (2003) and others by illustrating the relative influence of the physical environment on swimming. Smith Sound, Trinity Bay supports a large, persistent inshore spawning aggregation of Atlantic cod (Rose 1996). This aggregation provides a potential discrete, natal source of larvae to evaluate the potential contribution of larval swimming behaviour to cod dispersal through spatial and morphological analysis of field specimens. Trinity Bay is also characterized by high abundances of larvae of several other families, including *Scorpaenidae*, *Stichaeidea*, and *Osmerida*, providing additional tests of potential swimming contributions to spatial heterogeneity. The objective of this chapter is to evaluate possible active behavioural contributions by fish larvae to dispersal and connectivity through a combination of laboratory experiments, field observations, and hydromechanical principles. Specifically, I will address two main questions. First, could larval behaviour play a role in dispersal and therefore connectivity of Trinity Bay populations? Second, at what point during larval development does this contribution begin? I will address these questions utilizing the physical environment as a mechanistic framework in which to assess biological processes.

3.2 Methods

Sampling Protocol

Larval and egg data were derived from ichthyoplankton Tucker Trawl surveys conducted in Trinity Bay, Newfoundland during the spring of 2004 and 2006, and during the

summer of 2004. A total of 20 ichthyoplankton stations were sampled in a "bullseye" pattern radiating out from Smith Sound on the western side of Trinity Bay (Figure 3.1) in oblique hauls to ~40 m depth, thus encompassing the mixed layer (Laprise and Pepin 1995; Bradbury et al. 2001). The Tucker trawl was utilized because it has been shown to minimize the variability in catch estimates relative to other ichthyoplankton gear types (Pepin and Shears 1997). Although size and species-specific net avoidance could not be directly measured, the large sample volume collected by the Tucker trawl is designed to minimize any possible bias associated with net avoidance. Larvae were sampled and preserved in a buffered seawater and 4% formalin solution. Each sample was processed in its entirety for larvae and identified to species according to identification keys outlined in Fahay (2007). Once picked, larvae were stored in a 5% ethanol solution for further processing.

Allometric analysis

To test the hypothesis that larval growth trajectories reflect some optimization within the mechanical constraints placed by the fluid environment, I performed an allometric analysis on data obtained from a detailed library of larval Atlantic cod (*Gadus morhua*) images produced from larvae reared at the Joe Brown Aquaculture Research Facility of Memorial University (Guan Lu, unpublished data). Morphological data were recorded from the image library using a pixel/mm calibration in Image J image analysis software. Several morphological parameters were measured to the nearest 0.01 mm in each image. Total length was defined as the measurement from the most anterior tip of the body to the midlateral posterior edge of the hypural plate and was chosen as the preferred body size

index. Comparisons of growth of different body segments relative to the body size index can provide insight into possible functional relationships between morphology and larval development. The body area was taken as the entire surface area of the larval fish excluding the fins. Physiological and thrust areas were defined as the total surface area anterior or posterior to the distal portion of the gut, respectively (Figure 3.2). The physiological area was defined as the portion of body surface area from the anterior tip of the body to the distal portion of the gut. Physiological area was chosen for its utility as a possible metric to describe physiological development. The thrust area was defined as the area around the midlateral line extending anterior from the distal portion of the gut to the posterior edge of the hypural plate. Thrust area provides a useful metric to describe the functional surface area associated with swimming because the amount of water accelerated during tail undulation will be proportional to this surface area. Caudal height and body depth were defined as the minimum (at the caudal peduncle) and maximum heights of the fish respectively (Figure 3.2). Caudal height and body depth are useful metrics to describe streamlining, and therefore drag reduction of the larval morphology.

Standard length was used as an index of overall growth and regressed against several other growth parameters to detail how body shape changes throughout ontogeny. Shape changes were quantified by calculating exponential linear scaling factors according to the equation:

(1) $$y = aX^b$$

Where y is the dependent variable, a is a scaling constant, X is the independent variable (standard length) and b is the exponential scaling factor. Using $\log_{10}$ transformed data, the scaling factor $\boldsymbol{b}$ was calculated according to the equation:

$$\log_{10}(y) = \boldsymbol{b} \log_{10}(\mathrm{L}) + \log_{10}(a) \tag{2}$$

Once calculated, b can be compared to the isometric growth scaling factor b_0. The null hypothesis, isometry, assumes proportional growth among the morphometric factors being compared. When total length (L) is used as a body size index, expected isometric growth rates (b) would be linear and squared functions for length and surface area body parameters respectively. I used reduced major axis (RMA) regression so that a realistic model of the data could be constructed, acknowledging that random error can be associated with each of the variables, X and Y (Rayner 1985; McArdle 1988, 2003). RMA regressions were performed according to Sokal and Rohlf (1981). Estimates of b were then statistically compared to b_0 using 95% confidence intervals. If b_0 fell above or below the 95% confidence interval, then the parameter y was inferred to represent negative or positive allometric growth relative to body length, respectively. Allometric analyses illustrate changes in larval geometry throughout ontogeny. Given the expected changes in larval behaviour (Fisher et al. 2000) and interaction with the fluid environment (McHenry and Lauder 2006), the allometric analyses might also provide some insight as to the functional relationship between biological processes (i.e. swimming), morphology, and fluid interactions.

Using the image library provided by Guan et al. (2008), I determined direct morphological-kinematic relationships. Morphological parameters were regressed against critical swim speed and sustained swimming time (Guan et al. 2008), thus providing information needed to proved a more detailed morphometric-kinematic analysis, building upon basic models provided by Guan et al. (2008). The coefficient of determination (R^2) gives a quantitative measure of the variance explained in a statistical model. Each morphometric-kinematic model provides a unique value for R^2, however, error bars or statistical comparisons are not possible without further analysis. A bootstrapping algorithm developed in Minitab® 15, was used to create 1000 randomizations of R^2 estimates. This distribution was then utilized to generate error bars about the estimated R^2 developed from the morphometric-kinematic models. These estimates of error enable a realistic comparison of model predictive ability based on real data and are independent of any specific statistical error structure.

Observed Patchiness

Larvae obtained in the ichthyoplankton surveys, were identified to species and imaged at the Ocean Science Centre's Image Data Analysis Facility (IDAF). For each species, a maximum of 100 length measurements were derived from each station. Samples with an excess of 100 individuals of a single species were sub-sampled using a Motoda plankton splitter. Length was calculated from the images and a pixel per mm calibration using Image J® image analysis software, measured to the nearest 0.1 mm. Standard length was defined as the measurement from the anterior tip of the body to the midlateral posterior

edge of the hypural plate. Specimens were then separated into 1 mm size bins and displayed as size frequency distributions for each station.

Samples from May 2006 were also processed for zooplankton abundances. Specimens were identified to species where possible and sub-sampled to a minimum count of 300 individuals per sample using a Motoda plankton splitter. Linear kriging was utilized to increase the spatial resolution of sampling surveys by estimating total biomass between sample stations in Surfer® 8. The linear kriging method is advantageous as it provides a spatial estimate of biomass using data interpolated from all stations sampled (Papritz and Stein 1999). Preliminary examination of plots suggested strong differences between the eastern and western sides of the bay. Therefore, interpolated data from the kriging analysis divided into western and eastern Trinity Bay using associated GPS coordinates and Microsoft Excel. Mean abundances for east and west were plotted with 95% confidence limits to demonstrate spatial heterogeneity punctuated with a spatial bias to the eastern or western coasts of Trinity Bay.

Lloyd's (1967) index of mean crowding was used to determine spatial heterogeneity of larvae of different size classes in the sample grid (Figure 3.1). Lloyd's index (P) is defined as:

(3)
$$P = 1 + \frac{\sigma^2 - \bar{x}}{\bar{x}^2}$$

where $\bar{x}$ is the mean number of individuals and σ^2 is the population variance for the organisms counted in the size class. Lloyd's index provides a mechanism to determine the patchiness of a particular taxon, or in this case, size classes of a given taxon. Lloyd's index explains quantitatively how more frequently an individual occurs in a given sample relative to an individual from a randomly distributed population with the same mean density (Lloyd 1967). Because the calculation is independent of larval concentration, it is useful for comparing among years, areas, or even developmental stages. This flexibility and ease of interpretation of Lloyd's index has contributed to its use in studies on patchiness in the marine environment (Matsurra and Hewitt 1995; Stabeno et al. 1996; Methven et al. 2003; Bradbury et al. 2003)

The calculation of Lloyds index requires an estimate of population variance when the use of sample variance might not be appropriate. Several authors have estimated population variance by applying a negative binomial distribution to ichthyoplankton data (Lloyd 1967, Stabeno et al. 1996; Matsurra and Hewitt 1995) according to methods outlined by Bliss and Fisher (1953). The approach outlined in this chapter utilizes a negative binomial distribution to apply a maximum likelihood expression to the station count data, thereby allowing calculation of a dispersion parameter *k*. An iterative solution for *k* was then determined through the following equation:

(4) $$N \log_e[1 + \frac{\overline{X}_i}{k}] = \sum [\frac{f(X_i)}{k + X_i}]$$

Where N is the number of samples, (X_i) represents the sample mean and, $f(X_i)$ is the observed frequency of samples containing X individuals (Bliss and Fisher 1953). When necessary, data were pooled between surveys and size bins in order to obtain sufficient samples sizes (Bradbury et al. 2003). The dispersion parameter k was solved for using the Excel solver tool and equation (4). Because the Excel solver tool tends to remain on local minima, the initial estimate of k_2 (second moment of dispersion) was derived from according to the following equation:

(5)
$$k_2 = \frac{\overline{X_i} + \overline{X_i}^2}{S^2}$$

where S^2 is the sample variance and X_i represents the mean larval count for the specified size bin (Bliss and Fisher 1953). This initial estimate was used as a start point from which solver then calculated an estimate of k according to equation (4). The effectiveness of this estimation method was verified using data from Matsurra and Hewitt (1995) and was consistent with their calculated estimates values of k in all comparisons.

The estimate of k was then incorporated into Lloyd's index of patchiness (Maynou et al. 2006; Bradbury et al. 2003; Methven et al. 2003), simplifying Lloyds index equation to:

(6)
$$P = 1 + \frac{1}{k}$$

where P is an estimate of patchiness and k is the dispersion parameter estimated by excel solver with the maximum likelihood approach (equation 4). An estimate of P = 1

indicates the crowdedness of the population is equal to the mean density. Estimates of P greater than 1 denote how many more times crowded an individual is than a random distribution (Lloyd 1967). Standard error was estimated with k_2 according to equation (5) based on the number of 0 counts according to the following equation:

(7)
$$SE_p = \sqrt{\frac{(1-R)^{-k} - (1+kR)}{N[-\ln(1-R) - R]^2}}$$

where R is derived according to equation (8)

(8)
$$R = \frac{\bar{x}}{k + \bar{x}}$$

N is the number of samples, $\bar{x}$ is the sample mean and k is the dispersion estimate.

Hydrodynamic environment

The fluid environment around a particular larval fish was characterized by calculating the Reynolds number (Re) based on the formula outlined in (Brett 1964);

(9)
$$\mathrm{Re} = U_{crit} \frac{L}{\nu}$$

where U_{crit} = critical swim speed (m/s), L equals standard length in meters, corresponding the length of the fish parallel the flow of water moving past the body and ν is the

kinematic viscosity of seawater (m^2/s) . Total length (L), defined as the mean size within a 1 mm size bin, was used to calculate patchiness for a particular species (i.e. 0.00055 m for the 5-5.9 mm size bin). This mean length was also applied to the swimming parameter (U_{crit}) of the Reynolds number equation. Guan et al. (2008) defined critical swim speed (U_{crit}) as the potential swimming performance of the test subject. Larval fish at varying stages of development were placed in a swim tunnel and allowed to acclimate for 10-15 minutes under static conditions. Once acclimated, the current velocity was incrementally increased until the fish was no longer able to swim against the current and maintain position. The critical swim speed was then calculated following methods outlined in (Brett 1964):

(10)
$$U_{crit} = U + (\frac{t}{t_i})U_i$$

where U is the penultimate speed, U_i is the velocity increment (set at 1.0 cm/s), t is the time at the maximum sustained velocity increment, and t_i is the time interval for each increment (set at 120 seconds).

Critical swim speeds for Atlantic cod were derived from length-dependent swimming curves derived from image analysis and swim data reported in Guan et al. (2008).

Guan et al. (2008) developed a statistically significant multispecies model for swimming ability using total length as the predictive variable (R^2=0.90). The morphometric

kinematic equation of Guan et al. (2008) was then applied to estimate the length-dependent swimming ability of larvae of all other species.

(11) $$\text{Multispecies}_{U\text{crit(cm/s)}} = 0.79(L)-2.03$$

Where *L* is the standard length of the larvae measured in cm. Measurements of average surface (upper 5 m) and mixed layer (upper 40 m) temperature, salinity, and fluorometry were obtained from vertical CTD casts taken concurrently with each ichthyoplankton survey, with the exception of 2007 where the inner most stations were not able to be sampled. CTD casts were processed for the mixed layer (top 40 m) and analysed for spatial pattern using linear kriging analysis in Surfer® 8 and compared with spatial patterns of larvae throughout ontogeny. Kinematic viscosity (v) was calculated using a standard curve predicting kinematic viscosity of sea water for a given temperature derived from Fuiman and Batty (1997) (Figure 3.3). Average mixed layer temperature was utilized to calculate the kinematic viscosity of the ocean water during a given survey (Figure 3.4). Kinematic viscosity also changes as a function of salinity, however, average salinity differences among survey seasons were negligible, maximum difference of 0.7, and were therefore not considered (Figure 3.5).

The estimated swimming velocities from the morphometric kinematic relationships and average kinematic viscosities (described above) were then used to estimate Reynolds number for a specific a size range of larvae. Reynolds numbers calculated to be below 20 were inferred to represent a viscous environment (Gillis 2003), Re between 20 and 300

represented a transitional environment, and Re greater than 300 represented an inertial environment (Fuiman and Batty 1997, but see Discussion and Leis 2007).

Both Lloyd's index and Reynolds numbers were then estimated for larvae measured from the field using length as the linking factor in all equations. Overlaying the hydrodynamic environment information on patchiness data illustrates the linkages between the hydrodynamic environment and spatial heterogeneity in the field. These results support the hypothesis of this exercise that increased spatial patchiness is expected for late larval sizes concomitant with the transition to an inertial swimming environment more conducive to active behaviour (Re>300) (Figure 3.6).

To visualize observed spatial pattern as a function of larval ontogeny contour plots were created in Surfer® 8 using the linear kriging function. For each contour plot only one survey was utilized to demonstrate the pattern whereas Lloyds index calculations were based on combinations of survey rounds (i.e. multiple surveys collected at one time) Concentrations of larvae were binned into early middle and late using length as a proxy for larval development. Data from kriging analysis was divided two eastern and western Trinity Bay and presented as a mean ± standard deviation in order to illustrate how spatial association changes as a function on larval development.

3.3 Results

Allometric analysis

Allometric relationships determined from RMA regression indicated that two kinematic parameters – total body surface area and thrust area – exhibited positive allometric growth (slope > 2) relative to total length for larval cod (Figure 3.7 a,b). Physiological area and body depth exhibited isometric growth relative to total length (Figure 3.7 c,d). All models were significant ($\alpha < 0.01$) and demonstrated good fit in data with over 80% of the variance explained by the model parameters (Table 1).

Morphometric kinematic analyses also indicated strong relationships. For both kinematic parameters, models created using total length as a body size index demonstrated the strongest relationships, with coefficient of determination values of 0.97 and 0.91 for critical swim speed and sustained swimming respectively (Figure 3.8). Morphological parameters along the longitudinal axis (total length, thrust length, and physiological length) produced the highest predictive capacity for critical swim speed (Figure 3.9 a, summarized in Table. 3.2). Sustained swimming was best predicted by total length and parameters associated with the head and gills. Body depth and physiological area best predicted sustained swimming ability (Figure 3.9 b summarized in Table. 3.3). Models developed with caudal height had the lowest coefficients of determination with only 23 and 66% of explained variability for sustained swimming and critical swim speed respectively (Tables 3.2 and 3.3). Bootstrapping analysis of 1000 randomizations demonstrate significant overlap (R^2 ±1 standard deviation) in the predictive ability of

morphological parameters, however, there was increasing variability in the relationship as the predictive capacity decreased (Figure 3.9 a,b).

Field observations

Temperature observations, both in the surface and mixed layers, indicate strong seasonal differences in temperature with an observed 8 ^{o}C difference between May and July of 2004. Mixed layer temperatures within a year demonstrated markedly less seasonal warming, with only a 2 ^{o}C difference between May and July of 2004. Interannual differences exhibited similar patterns with a 2.5 ^{o}C and 2 ^{o}C maximum difference between surveys in May 2004, 2006, and 2007, for the surface and mixed layer respectively (Figure 3.4).

Data from all years and seasons indicate the presence of colder water associated with the western side of Trinity Bay in the vicinity of Bonaventure Head. On average, a 0.5 ^{o}C difference was observed between the area immediately surrounding Bonaventure Head and the survey average for both surface and mixed layer measurements (Figures 3.10 and 3.11).

Variability in salinity indicated a near constant salinity among seasons and years. Seasonally a -0.08 and 0.15 difference in salinity was observed between May and July 2004 for the surface and mixed layers respectively. No consistent salinity gradient was

observed between the eastern and western portions of Trinity Bay, which did not differ in salinity by more than 0.07 during any survey (Figure 3.12).

Fluorometric measurements of chlorophyll A concentrations were, on average, 0.4 µg/L higher on the western side of Trinity Bay compared to the eastern side. In all surveys except May 2007, the highest fluorescence values were associated with the area immediately surrounding Bonaventure Head where the coldest surface waters also occurred (Figure 3.13).

For the May 2006 survey which was processed for zooplankton in addition to ichthyoplankton, there was a high spatial association (Figure 3.14) of total zooplankton abundance (#of individuals per tow) with the western side of the bay in the vicinity of the cold upwelling. Acknowledging that the zooplankton data is limited to this survey alone, there are associations of peak zooplankton abundance with cold water upwelling (Figures 3.10 and 3.11) and increased fluorescence (Figure 3.13), which were features also observed in the 2004 sample surveys.

Observed Patchiness

Spatial analysis of Lloyd's index, as a function of ontogenetic development, was limited in that only Atlantic cod, *Gadus morhua*, had sufficient numbers of eggs to perform patchiness analysis that included the egg stages. Nonetheless, comparisons of patterns in larvae for multiple species indicated a general '*U*'-shaped pattern in patchiness through

larval ontogeny (Figures 3.15 and 3.16). Patchiness was highest for the smallest and largest larval sizes collected in the ichthyoplankton surveys. Generally the patchiness pattern decreased at intermediate larval sizes. For Atlantic cod, patchiness of early larvae was similar to patchiness in egg stages. Only in radiated shanny (*Ulvaria subbifurcata*) and Atlantic seasnail (*Liparus atlanticus*) was there was no pronounced increase in patchiness for the largest size grouping. The standard error estimated about each mean varied from 0.05 in witch flounder (*Glyptocephalus cynoglossus*) to 3.2 in Atlantic seasnail. The effect of zero counts (stations where no larvae of any size were caught) had mixed effects depending on the species in question, either exaggerating patchiness estimates for species with large numbers of larvae (i.e capelin) or reducing the estimates for larvae with lower numbers of larvae (i.e.redfish). Despite the variability in direction of patchiness estimate change, the overall pattern with size was similar irrespective of whether zero values were included. To be consistent with other authors who have used this method (e.g. Stabeno et al. 1996; Bradbury et al. 2003; Maynou et al. 2006), and to account for different responses depending on the species, all zero stations were removed from the analyses presented here.

The spatial heterogeneity as a function of larval ontogeny, for 8 species of larvae show that, as would be expected in the patchiness analysis (Figures 3.15 and 3.16), spatial patterns suggest that early and late larval stages are more defined and visually patchier than intermediate stages. An axis was drawn down the center of the sampling grid to divide Trinity Bay into eastern and western regions. Redfish (*Sebastes* spp.), radiated shanny, and witch flounder were all significantly more abundant on the eastern side of

Trinity Bay throughout larval ontogeny. Arctic shanny (*Stichaeus punctatus*.) and Atlantic seasnail shifted between the east and west divide during the latest defined stage. The remainder of the species were significantly more abundant on the western side of Trinity Bay throughout ontogeny (Figures 3.17 and 3.18). Larger individuals of Atlantic cod, American sandlance (*Ammodytes americanus*), capelin (*Mallotus villosus*), redfish, and Atlantic seasnail were associated with the western side of Trinity Bay near Bonaventure Head, which is characterized by upwelling (Figures 3.10 and 3.11), elevated fluorescence (Figure 3.13) and greater zooplankton abundance (Figure 3.14) relative to other areas sampled in the bay.

Kriging data provided a useful mechanism to smooth out bias in the sampling grid, such as highly clustered stations near the natal source of cod larvae in Smith Sound. However, the kriging process uses all available data to estimate values for spatial locations where samples were not taken. This procedure provides a reasonable estimate of mean egg concentration but provides an unreliable estimate of variance for each side of the bay because variance estimates for the east and west side of the bay are not independent. To determine if this statistical violation impacted the spatial interpretation, raw data on Atlantic cod and American sandlance (figure 3.17), was divided into east and west stations and kriged individually. This manner of kriging provided a mechanism to compare means without the problem of non-independent variance. In all tests, the means and variances changed by less than 5% and in no cases did the interpretation of the results change. Although the analyses presented defy the assumption of independent variance, this secondary comparison suggests that the results are meaningful and provide a

reasonable mechanism to address spatial patterns despite a spatial bias in distribution of sampling stations.

Hydrodynamic environment

Total length demonstrated the greatest predictive capacity for kinematic potential of all morphometric variables available for the analysis (Figures 3.9). This finding is consistent with previous studies (e.g. Muller and Videler 1996; Guan et al. 2008) and lends confidence to the use of length as a linking parameter between field length distribution data and hydrodynamic theory. The Reynolds number, as calculated from equation 9, is a product of the swimming speed, length, and the kinematic viscosity of water. Critical swim speeds (U_{crit}) for Atlantic cod larvae of a given length (TL) were calculated according to:

(12,) $$U_{crit\,(cm/s)} = 16.273(Log_{10}TL_{(mm)}) - 10.262$$

Unfortunately swim data and corresponding images for larvae of other species obtained in the ichthyoplankton survey were not available. To estimate the swimming capacity of these larvae, a multi-species morphometric kinematic model based on larval length and measured swimming speeds (from Guan et al. 2008) was utilized, based on equation 11.

The only unresolved component of the Reynolds number calculation is the kinematic viscosity of water. The kinematic viscosity is the molecular viscosity of seawater which

has a well-known temperature dependence (Fuiman and Batty 1997). The viscosity of seawater varies from 1.79×10^{-6} m^2/s at 0 °C to 1.40×10^{-6} m^2/s at 10 °C (Figure 3.3). Larval counts did not yield sufficient numbers to estimate patchiness reliably for individual surveys. This limitation necessitated the pooling of survey data, including the temperature data derived from CTD casts (see Figure 3.4). The mean temperature for the mixed layer (top 40 m) at all stations during all surveys was utilized to calculate the kinematic viscosity for all surveys according to the standard curve (Figure 3.3). Clearly, this method ignores between-survey variability (Figure 3.4), however, if the extreme high and low temperatures are used from the field, the estimate of Re changes by only ~3.5%, and therefore has no substantive impact on data interpretation. Mean temperature among surveys yielded an average kinematic viscosity of 1.714×10^{-6} m^2/s (s.d. = 0.138).

Data from equations 11 and 12 were used with binned mean lengths to predict Reynolds numbers according to equation 9. An iterative solution for the length at which Reynolds numbers would equal 20 and 300 was used to determine the boundaries of hydrodynamic regimes (Fuiman and Batty 1997). For Atlantic cod the transition between the viscous ($Re<20$) and the intermediate ($20<Re<300$) flow regimes occurs at 4.5 mm total length. The transition into the inertial flow regime occurs at 9.3 mm total length. For all other species of larvae collected, the transition from the viscous environment was estimated to occur at 3.7 mm and into an inertial environment at 9.5 mm (Figures 3.15 and 3.16).

Several consistent patterns are apparent with respect to patchiness in the context of hydrodynamic environmental transitions (Figures 3.15 and 3.16). For all species except

Atlantic seasnail, a rise in patchiness occurred leading up to or at the transition to the inertial environment (Re>300). Variability in the estimate of patchiness also decreased in general after this critical transition (Figures 3.15 and 3.16). Estimates of patchiness for the Atlantic seasnail decreased throughout ontogeny with later sizes approaching random or uniform distribution (Lloyds index = 1).

3.4 Discussion

The role of dispersal during the larval phase in structuring the connectivity of populations has been at the forefront of many marine ecological studies (e.g. James et al. 2002; Levin 2006). Population connectivity has particular importance in fisheries management approaches (Yao 1986; Schillinger et al. 2000; Baumann et al. 2003; Swearer et al. 1999; Crowder et al. 2000) and marine conservation design (Cowen et al. 2000, 2006). Increasingly, researchers have examined the role of active swimming as a form of behaviourally-mediated dispersal rather than as a simple passive advective process (Wolanski et al. 1997; Cowen et al. 2000; Leis et al. 2007b). Partitioning the role of active and passive processes is required for robust predictive population models (Bradbury et al. 2003). An analysis of larval swimming ability is needed in order to evaluate the potential importance of active behaviour to larger-scale dispersal and connective processes (Guan et al. 2008). Laboratory studies can provide useful insight into this question but fall short of direct applicability to the dynamic environmental conditions observed in the field (Leis and Stobutzki 1997). Hydromechanical theory provides a bridge between laboratory studies and field observations. This bridge can shed

clarity on the applicability of laboratory studies to field-based predictions in the absence of any actual field measurements of directed movements.

Morphological and kinematic considerations

The effects of morphology can have implications for the movement of organisms and can therefore have pronounced ecological consequences (Koehl 1996). The relationship between morphology, swimming, and the hydrodynamic environment has been highlighted by several authors (e.g. Webb and Weihs 1986; Fuiman and Batty 1997; McHenry and Lauder 2006). Given that the hydrodynamic environment plays a significant role in limiting the swimming ability of this life history stage, it was hypothesized that individuals would exhibit positive allometric growth associated with the longitudinal axis in greater proportion to the rest of the body, in order to escape the viscous flow environment (Webb and Weihs 1986). However, the allometric growth patterns suggested by Webb and Weihs (1986) were not found in my analysis for Atlantic cod. Total body surface area and thrust area both scale positively with total length (RMA_{slope} 2.29 and 2.10 respectively), whereas physiological area and body depth scaled isometrically with total length (RMA_{slope} 2.17 and 1.03 respectively). These patterns do not fit the hydrodynamic prediction of Webb and Weihs (1986) but are generally consistent with observations of Muller and Videler (1996), who found that growth in gadiform volume was positively allometric compared to total length.

McHenry and Lauder (2006) suggested that the transition between hydrodynamic environments might take place on a time scale that does not permit the concomitant

change in body geometry to conform to the scenario outlined by Webb and Weihs (1986). They suggested instead that early larvae might exhibit morphologies which are not optimized for the viscous regime but instead are optimized for later stages of larvae which actively swim in the inertial environment. Koehl (1996) reiterated the same concept, acknowledging that often the smallest organisms exhibit the greatest array of morphologies, many of which might play a novel role in processes such as locomotion in different hydrodynamic environments. This argument is supported by my results considering that the thrust producing posterior two thirds of the body (thrust surface area) grows proportionally faster than total length (RMA_{slope}=2.10). This morphological growth pattern suggests that a larva enters the inertial fluid environment with larger proportional thrust-producing surface areas, relative to length, despite the fact that this morphology adds viscous drag to the animal at that point of its development. The concurrent isometric growth trends associated with body depth and physiological area relative to total length,could be involved with drag reduction, which is particularly important in the viscous swimming environment. McHenry and Lauder (2006) note that viscous drag is related to skin surface area. Many fishes are streamlined to minimize drag associated with surface area. A simple morphometric model for streamlining is the ratio of total length to maximum body depth. (Webb and Weihs 1986). We find an absence of any allometric growth trajectory associated with these body parameters is likely related to streamlining growth trajectories expected in small swimming organisms such as larval fish. This observation suggests a compensation for the positive allometry associated with the thrust area. Though length does exhibit positive allometric growth, as suggested by Webb and Weihs (1986), the growth trajectories observed for Atlantic cod fit theory

based on pre-optimization for hydrodynamic environments encountered later in development. These results agree with recommendations from previous authors (Webb and Weihs 1986; Fuiman and Batty 1997; McHenery and Lauder 2006) that morphological growth trajectories should be closely linked to the local hydrodynamic environment.

Locomotion is intrinsically related to organism morphology. Morphometric kinematic analysis demonstrated that total length was the best predictor of sustained swimming ability and critical swim speed in agreement with work presented by previous authors including Muller and Videler (1996). Given that total length is the best predictor of both swimming endurance (by proxy, sustained swimming) and maximum swimming performance (critical swim speed), its usage in spatial analysis is well founded. The morphometric kinematic analyses for sustained swimming yielded body components associated with the anterior extremities, physiological area, and body depth of the larvae have the next highest predictive capacities. This result is not surprising given that larval swimming endurance is mediated by the physiological capacity (Leis and Clark 2005). The morphological association of body depth and physiological surface area with the respiratory and digestive systems of larval fish makes them good proxies for physiological ability, explaining their predictive association with sustained swimming. Critical swimming ability was best defined by the linear measurements of total length, thrust length, and physiological length. This is not unexpected given that the fastest possible swimming ability should be related to the maximum tail amplitude (Webb and Weihs 1986) which in turn will be defined by linear measures such as thrust length.

These analyses provide useful insight into the relationship between morphology and kinematics. They also demonstrate that total length is a very useful morphometric for illustrating swimming abilities and swimming-related processes.

Spatial heterogeneity in the field

The analysis of spatial heterogeneity as a function of larval length suggests that swimming ability may play an increasingly important role through ontogeny. Estimates of patchiness, with the exception of Atlantic seasnail, demonstrated an increase in spatial patchiness as larvae grew. The characteristic U-shaped pattern described by several authors (Stabeno et al. 1996 and others) is clearly evident in seven of the eight abundant species collected during ichthyoplankton surveys in Trinity Bay. High spatial patchiness at small sizes is consistent with the assertion that small larvae experience a viscous environment and like eggs, act essentially as passive particles (Fisher and Bellwood 2000; Bradbury et al. 2003). This trend is clearly seen in Atlantic cod, where patchiness in early stages of larvae is very similar to that for egg stages. However, if passive processes alone dictated spatial pattern, there would be no reason to expect the consistent high patchiness at early and late size ranges and low patchiness during intermediate sizes across species observed in my study.

Contour plots of field data provide a method to spatially interpret patchiness patterns. These plots demonstrate how the larval spatial distributions change as a function of larval development, by proxy size of the larvae. For multiple species a consistent trend of lower patchiness for intermediate, relative to small and large size ranges, was observed.

Bradbury et al. (2003) noted that the late larval stages of several species were associated with localized areas of heightened productivity and were counterintuitive with a passive model given the ambient flow conditions in Placentia Bay. Bradbury et al. (2003) argued that because these larvae were associated 'upstream' of their predicted location, active behavioural modification of passive drift was necessary to explain spatial pattern. In my study, Atlantic cod, American sandlance, capelin, and Atlantic seasnail were associated with the western side of Trinity Bay throughout larval ontogeny. Redfish and Arctic shanny both show increased mean abundance associated with the western side of Trinity Bay as a function of size. Only witch flounder and radiated shanny lack any evidence of increased mean abundances associated with western Trinity Bay. The consistent association of witch flounder with the east coast of Trinity Bay, in contrast, shows no evidence of any net movement.

All of these observations are inconsistent with a passive explanation given the mean bay-scale current conditions. Circulation modelling by Yao (1986) and Tittensor et al. (2001; 2002) illustrate that circulation patterns are strongly influenced by an inshore branch of the Labrador Current. Current meter observations indicate that the mean flow direction is typically equal to the variance (Tittensor et al. 2001; 2002). There is, nonetheless, a clear pattern of water entering on the west and exiting on the eastern coast. Flow variability, primarily driven by wind stress (Davidson et al. 2001), produces complex patters of current response that is dominated by a complex upwelling-downwelling cycle and a Kelvin wave. A counter clockwise gyre can also be observed near the mouth of Smith Sound, which exhibits some of the strongest flow measurements known or the Trinity

Bay (Figure 2.2, from Tittensor et al. 2002). Passive residency times in Trinity Bay, based upon particle tracking calculations made using the Candie model (Davidson et al. 2001), in Trinity Bay are on the scale of days to weeks (B. deYoung, personal communication, Department of Physics and Physical Oceanography Memorial University of Newfoundland, St. John's NL, A1C 5S7). Larvae of all species, with the exception of radiated shanny and witch flounder, occur in locations that are "upstream" of where they would occur if passive processes alone dictated spatial pattern. The static spatial distribution of witch flounder is also inconsistent with a passive model. Swimming ability has been shown to scale positively with length for numerous fish species (e.g. Williams et al. 1996). The upstream spatial association of larger larvae, who are likely better swimmers, leads to the parsimonious conclusion that active larval behaviour might influence spatial pattern.

Hydro-mechanical considerations

The hydrodynamic environment dictates the physical boundaries placed by fluids around an organism and, for small organisms, can place major restrictions on its locomotor abilities (Fuiman and Batty 1997). Integration of the morphometric, kinematic, and spatial analyses allows interpretation of field observations in light of the hydromechanical constraints experienced by larvae. This approach is particularly useful in inferring whether swimming influences the spatial heterogeneity observed in many field situations. Low Reynolds numbers (Re <20) characterize environments where swimming is limited by viscous drag (Fuiman and Batty 1997). The point at which an organism operates in a clearly inertial zone (Re >300) has generated debate. Early estimates set the transition

point at a Re number of 200 (e.g.Webb and Weihs 1986), however, more recent observations and modeling set the Re transition at 300 (Fuiman and Batty 1997) or 1000 (McHenry and Lauder 2005). The transition estimate of Fuiman and Batty (1997) and a lower limit estimate by McHenry and Lauder (2005) was used in this analysis. Using the field data and morphometric kinematic models, Re values for the viscous and inertial transitions were estimated for each species and then overlaid onto the estimates of spatial patchiness. Generally in cold ocean species larvae hatch into a viscous environment (Re<20) and transition (20<Re<300) into an inertial hydrodynamic environment (Re>300), where swimming becomes efficient (Guan et al. 2008). The pattern in spatial heterogeneity, provided by Lloyd's indices, indicates an increase in patchiness associated with the transition into the inertial hydrodynamic environment, suggesting that spatial distributions of larvae in the field are a result of swimming behaviour. The transition to the inertial flow environment was associated with an increase in spatial patchiness for all species except Atlantic seasnail. For Atlantic cod, capelin, redfish and Arctic shanny the transition into a viscous environment coincided with a 3-8 fold increase in patchiness. For these species a strong spatial association with the western side of the bay is clearly evident. American sandlance and radiated shanny did not demonstrate the marked increase in patchiness associated with the transition to the inertial environment but patchiness increased after the transition, as predicted with active swimming. Atlantic seasnail patchiness was nearly uniform (Lloyds index of 1), suggesting that behavioural contributions are less important or vary less with development, or that the multispecies model for predicting maximum swim speed is inappropriate for this species and the transition to the inertial flow environment had not yet occurred.

Results from the hydrodynamic spatial pattern analysis were strikingly similar to conclusions from other studies on spatial patchiness and critical swimming development points during larval development. Frank and Leggett (1982) looked at dispersal of larval capelin and estimated that 10 mm total length represented a critical developmental stage at which larval capelin would be able to migrate vertically and potentially use vertical shear to influence their dispersal. Stabeno et al. (1996) demonstrated a minimum larval size of 10 mm was necessary to maintain observed patch sizes for walleye pollock (*Theragra chalcogramma*). More recently, Bradbury et al. (2003) estimated the minimum larval size required to maintain patch sizes observed in Placentia Bay was also 10 mm. Guan et al. (2008) found that shorthorn sculpin (*Myoxocephalus scorpius*) larvae were significantly better swimmers at hatch than Atlantic cod. This difference was partially explained by the larger hatch size of shorthorn sculpin (10.84 mm) compared to that of cod (5.25 mm). At the larger hatch size, shorthorn sculpin were swimming in a near-inertial environment, whereas cod only achieved comparable swim speeds at a minimum length of 10 mm. The present analyses suggest that the transition into an inertial environment was estimated as a total length of 9.3 mm for Atlantic cod and 9.5 mm for the other species examined. The 10 mm threshold (Frank and Leggett 1982; Bradbury et al. 2003) might be partially explained by the critical hydrodynamic shift suggested by this study. The earlier onset, 5-8 mm length, suggested by Leis (2007a) can be explained by an earlier transition to the inertial swimming environment due to warmer water temperatures and therefore lower kinematic viscosities (~45% decrease with a 15 ^{0}C increase in temperature). The swimming comparison between different size at hatch among species from Guan et al. (2008) and the present study of field spatial distributions

provide compelling evidence that swimming ability within the context of the hydrodynamic environment could contribute substantially to larger-scale population structure.

Patchiness: Does active behaviour play a role?

Morphometric, kinematic, hydrodynamic, and field spatial data support the hypothesis that swimming influences spatial patchiness during the early life history of larval fish. Patchiness, in a broad sense, is usually a product of the spatial patchiness of elements of the fish's environment such as food resources, predators, or passive influences such as oceanographic features (Lloyd 1967). It is unlikely that larval patchiness is simply a product of passive processes, given that field distributions are inconsistent with expectations based on passive drift.

How are these spatial patterns produced? Given that passive circulation alone cannot explain spatial pattern, there are three other likely biological processes that could explain the data. Active swimming is one possibility, but differential mortality could also occur, either as a result of spatially heterogeneous predation patterns or as a result of differences in availability of food resources. In order to partition the role that active swimming could play in explaining patchiness patterns, predation and food availability must both be addressed.

Predation could cause heterogeneous distributions of larvae because it can directly influence spatial patterns in ichthyoplankton abundances. Size-dependent predation is

particularly relevant to this analysis because this study analyzes spatial heterogeneity as a function of ontogeny. Bradbury et al. (2003), Baumann et al. (2003), and Pepin et al. (2002, 2003) examined spatial patterns of ichthyoplankton larvae in Newfoundland embayments. All of these studies noted that juvenile or adult capelin (*Mallotus villosus*) were likely the most dominant planktivorous fish in their respective systems. Baumann et al. (2003) carried out acoustic surveys in Trinity Bay to identify the spatial distribution of capelin, and their survey noted a temporally-consistent and strong spatial association of juvenile and adult capelin with the western side of Trinity Bay. These distributions are very similar to the patterns observed for larvae of several of the dominant species reported here. The assumption concerning the effect of predators and patchiness is that predators might influence prey distribution by feeding and lowering prey concentrations in areas where the predators are most abundant, therefore influencing spatial heterogeneity. If this were true, then higher larval densities would be expected away from a likely source of predators and the anecdotal evidence provided by Baumann et al. (2003) does not show this. Likewise, neither Baumann et al. (2003) nor Bradbury et al. (2003) detected any evidence of size-dependent mortality in their respective study systems. If size-dependent mortality is not a major factor, then the U-shaped pattern in patchiness is less likely to be solely a product of mortality and predation. In addition, the ontogenetic shift in spatial distribution to areas previously unoccupied for multiple species included in this analysis, is inconsistent with the hypothesis that predation alone produces spatial heterogeneity in the field data. Although predation cannot be fully dismissed, several pieces of evidence from this thesis suggest that swimming is a greater contributor to heterogeneous distributions of larvae.

Food resources are a fundamental component of any population or community. Several authors have formalized hypotheses that highlight the role of food resources in structuring marine pelagic larval distributions including the "stable ocean" (Lasker 1978), "member vagrant" (Iles and Sinclair, 1982), "match mismatch" (Cushing 1990), "right site" (deYoung and Rose 1993), and "ocean triad" hypotheses (Bakun 1996). This array of frameworks that draw on multiple biological and oceanographic fields are all linked by food availability and demonstrate the integral role spatial heterogeneity of food resources plays in larval survival. In terms of contributions to spatial heterogeneity, abundant food resources can concentrate organisms into patches (Lloyd 1967) or food-limited areas can lead to mortality. Pepin and Penny (2000) demonstrated in an adjacent Newfoundland bay, Conception Bay, that larval fish consume less than 0.1% of available microzooplankton, suggesting that starvation is extremely unlikely to contribute to spatial heterogeneity. Bochdansky et al. (2008) concluded that environmental factors regulating predator-prey encounter rates has a direct positive relationship with larval growth and survival. The western side of Trinity Bay near Bonaventure Head is characterized by persistent upwelling observed in my study as well as several others from past years (Yao 1986; Schillinger et al. 2000; Tittensor et al. 2001,2002; Baumann et al. 2003). Associated with this upwelling feature was heightened chlorophyll concentrations and zooplankton abundances. The primary food source for these fish larvae is likely microzooplankton (Pepin and Penny 2000) which was not directly sampled with the Tucker trawl. However microzooplankton are often associated with increased productivity and larger zooplankton are associated with areas of microzooplankton.

Moreover, the eggs of copepods that are sampled effectively with the Tucker trawl are an important potential food source for larval fish. Therefore, Although the upwelling region where late stage larvae were most abundant might represent a region of optimal habitat in Trinity Bay for pelagic larvae.

This prospect raises the question of whether larvae can actively swim and mediate their geographic locale. Larval fish have increasing sensory capabilities as they progress through ontogeny (e.g. Kingsford et al. 2002). Work on reef fish behaviour has demonstrated that larvae have directional swimming abilities that may allow them to cue in on features 10's to 100's of meters away (Leis and Carson-Ewart 1999, 2003). These examples, along with the evidence provided by laboratory and field data, illustrate that the spatial heterogeneity observed in larval fish in Trinity Bay may reflect an active swimming contribution from the larvae to take advantage of favourable local conditions.

Summary

Morphometric kinematic analysis of larval cod suggests a growth pattern that optimizes swimming efficiency as larvae enter an inertial hydrodynamic environment (Muller and Videler 1996). In my study, total length was the best morphometric predictor of swimming ability of Atlantic cod for critical swimming speed and sustained swimming ability. Spatial analysis that used total length as a proxy for ontological development revealed *U*-shaped patchiness estimates that are consistent with high patchiness in early and late stage larvae and juveniles as has been reported in previous studies (e.g. Stabeno et al. 1996; Methven et al. 2003; Bradbury et al. 2003). The peak in patchiness associated

with the most developed larvae collected in my samples coincided with the onset of the inertial swimming environment.

Field distributions demonstrated a spatial association of larval fishes with western Trinity Bay throughout ontogeny and, in some cases, an east-west shift from early to late stage larvae. Both of these patterns were inconsistent with predictions based on passive transport within the predominant circulation within the bay, therefore suggesting that patterns were not a result of passive physical processes. Persistent upwelling on the western side of Trinity Bay was noted on multiple occasions, and was characterized by elevated fluorescence and zooplankton biomass that characterize favourable habitat for larval fish.

Larval behaviour has been shown to mediate large-scale processes such as dispersal and connectivity in coral reef systems (e.g. Leis et al. 2007a). The concomitant presence of late-stage larvae and upwelling that coincide with the transition into an inertial hydrodynamic environment suggests that active swimming behaviour by larval fish as small as 15 mm or less can influence exhibited dispersal patterns and thus potentially contribute to population connectivity. Results from this study suggest that the onset of active contributions to spatial pattern coincided with the transition from viscous to inertial flow environments. This analysis is particularly relevant for cold ocean species where hydrodynamic constraints associated with the fluid environment are potentially strongest.

3.5 References

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Table 3.1 Allometic growth comparisons larval Atlantic cod (*Gadus morhua*). Reduced major axis regression equations presented as: Log_{10} (dependent variable) = b_{RMA} $\log_{10}$ (total length) + $\log_{10}$ (**a**)/. B_o is the isometric scaling rate. b_{lower} and b_{upper} represent 95% confidence intervals $t_{0.01,n-1}$

Dependent variable	b_{RMA}	b_{lower}	b_{upper}	B_o	a	r^2	p	n	Allometric relationship
Body area	2.29	2.13	2.47	2	-0.23	0.93	0.00	135	Positive
Thrust area	2.10	2.04	2.60	2	-0.30	0.81	0.00	135	Positive
Physiological area	2.17	1.98	2.36	2	-0.23	0.90	0.00	134	Isometric
Body depth	1.03	0.89	1.14	1	-0.12	0.80	0.00	173	Negative

Table 3.2 Ordinary least squares regression analysis for critical swim speed and morphological parameters on Atlantic cod (*Gadus morhua*). Regression equations follow: Independent variable = b_{ols} (Metric) + **a**. Coefficient of determination (r^2) values are presented with ± 1 bootstrapped standard deviation.

Independent variable	b_{ols}	*a*	r^2	*p*	*n*
Total Length	0.74	-1.71	**0.81** (± 0.03)	0.00	94
Thrust length	1.77	-3.11	0.80 (± 0.03)	0.00	71
Physiological length	1.48	0.73	0.78 (± 0.04)	0.00	71
Body area	0.37	2.19	0.75 (± 0.04)	0.00	71
Physiological area	0.56	2.05	0.73 (± 0.05)	0.00	71
Thrust area	1.00	2.52	0.71 (± 0.04)	0.00	71
Body depth	3.90	-1.72	0.67 (± 0.04)	0.00	94
Caudal Height	10.19	1.54	0.66 (± 0.04)	0.00	71

Table 3.3 Ordinary least squares regression analysis for weekly means sustained swimming and morphological parameters on Atlantic cod (*Gadus morhua*). Regression equations follow: Independent variable = b_{ols} (Metric) + **a**. Coefficient of determination (r^2) values are presented with ± 1 bootstrapped standard deviation.

Independent variable	b_{ols}	*a*	r^2	*p*	*n*
Total Length	4.87	-37.1	**0.91** (± 0.04)	0.00	5
Body depth	28.9	-35.3	0.91 (± 0.05)	0.00	5
Physiological area	4.56	-9.94	0.89 (± 0.06)	0.00	5
Thrust length	11.1	-35.9	0.88 (± 0.1)	0.00	5
Body area	3.51	-10.9	0.81 (± 0.07)	0.00	5
Thrust area	12.3	-10.5	0.79 (± 0.10)	0.00	5
Physiological length	12.0	-33.2	0.73 (± 0.13)	0.00	5
Caudal Height	32.1	-3.26	0.23 (± 0.25)	0.00	5

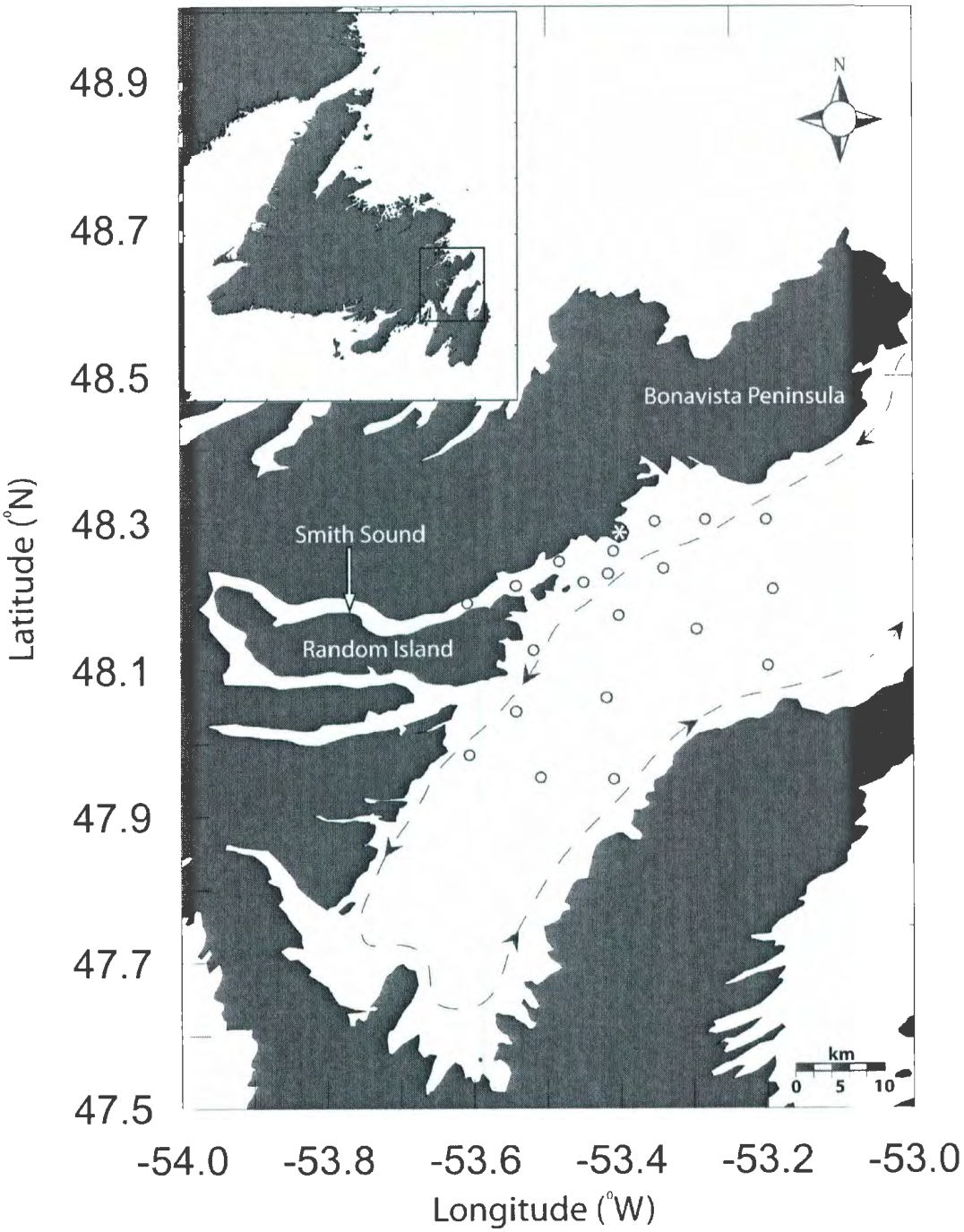


Figure 3.1 Trinity Bay ichthyoplankton survey array (O) sampled in May 2004/2006 and July 2004. Inset shows position of Trinity Bay relative to Newfoundland and Labrador. * symbol refers to Bonaventure Head. Dashed line represented mean passive flow conditions.

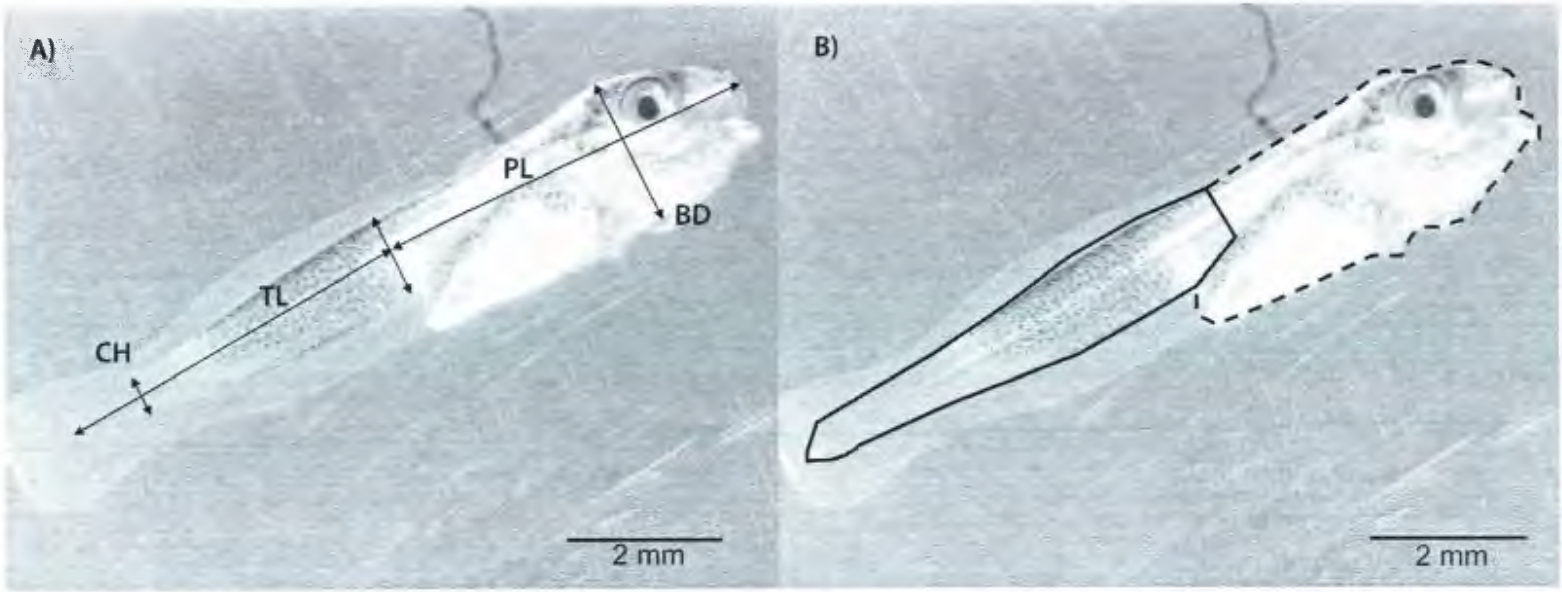


Figure 3.2 Image depicting larval morphological analysis. **A)** Morphometric parameters used in allometric and kinematic analysis' where CH = caudal height, ThL = thrust length, PL = physiological length, BD = body depth and total length = TL+PL. **B)** Body area defined as the total surface area of the larva excluding the fins (both shaded areas). Dashed line polygon defines the physiological area and solid lined polygon defines the thrust area. Refer to Methods (Section 3.2) for a breakdown of morphological boundaries for image analysis.

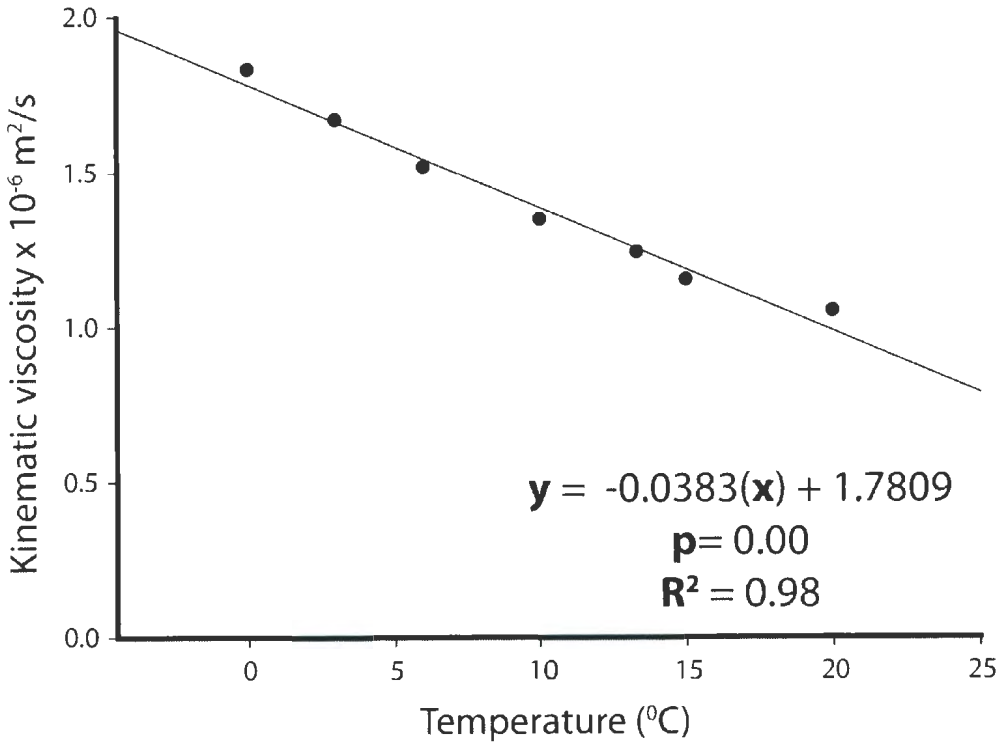


Figure 3.3 Kinematic viscosity of seawater standard curve based on temperature, data obtained from Guan et al. (2008) and Fuiman and Batty (1997).

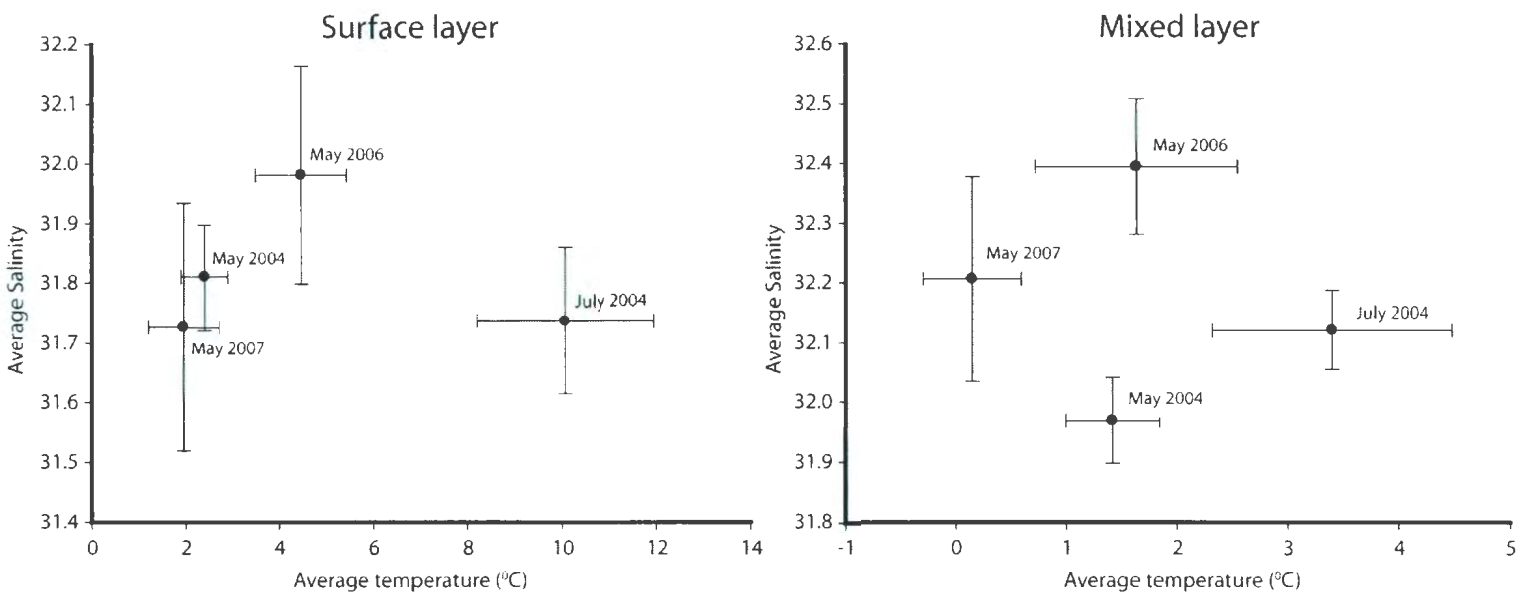


Figure 3.4 Average mean salinity vs. temperature (± 1 standard deviation) for each Trinity Bay ichthyoplankton survey 2004 – 2007. Surface layer data includes all measurements up to and including 5 m depth. Mixed layer data includes all measurements up to and including 40 m depth.

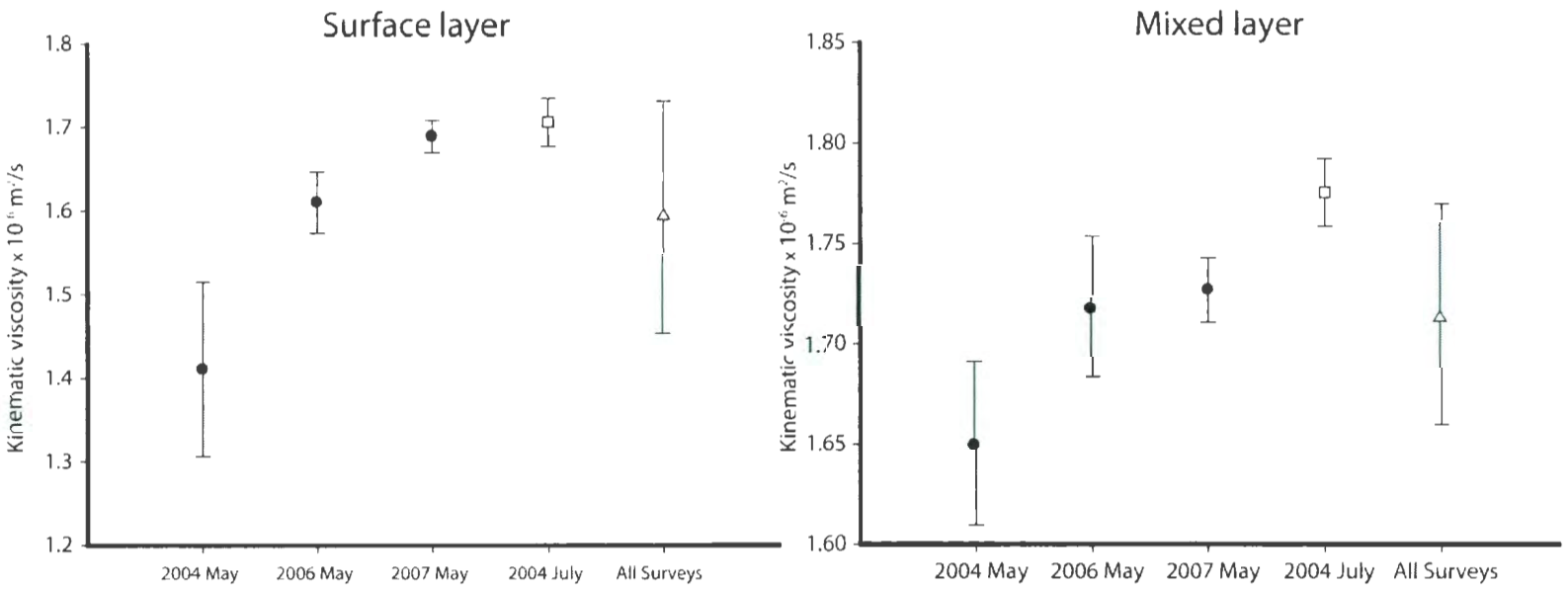


Figure 3.5 Average kinematic viscosity (ν) ($\pm$ 1 standard deviation) based on Trinity Bay survey averages. A) ν based on average temperatures in the surface layer (top 5 m) for each survey and between surveys B) ν based on average mixed layer temperatures (top 40 m) for each survey and between surveys.

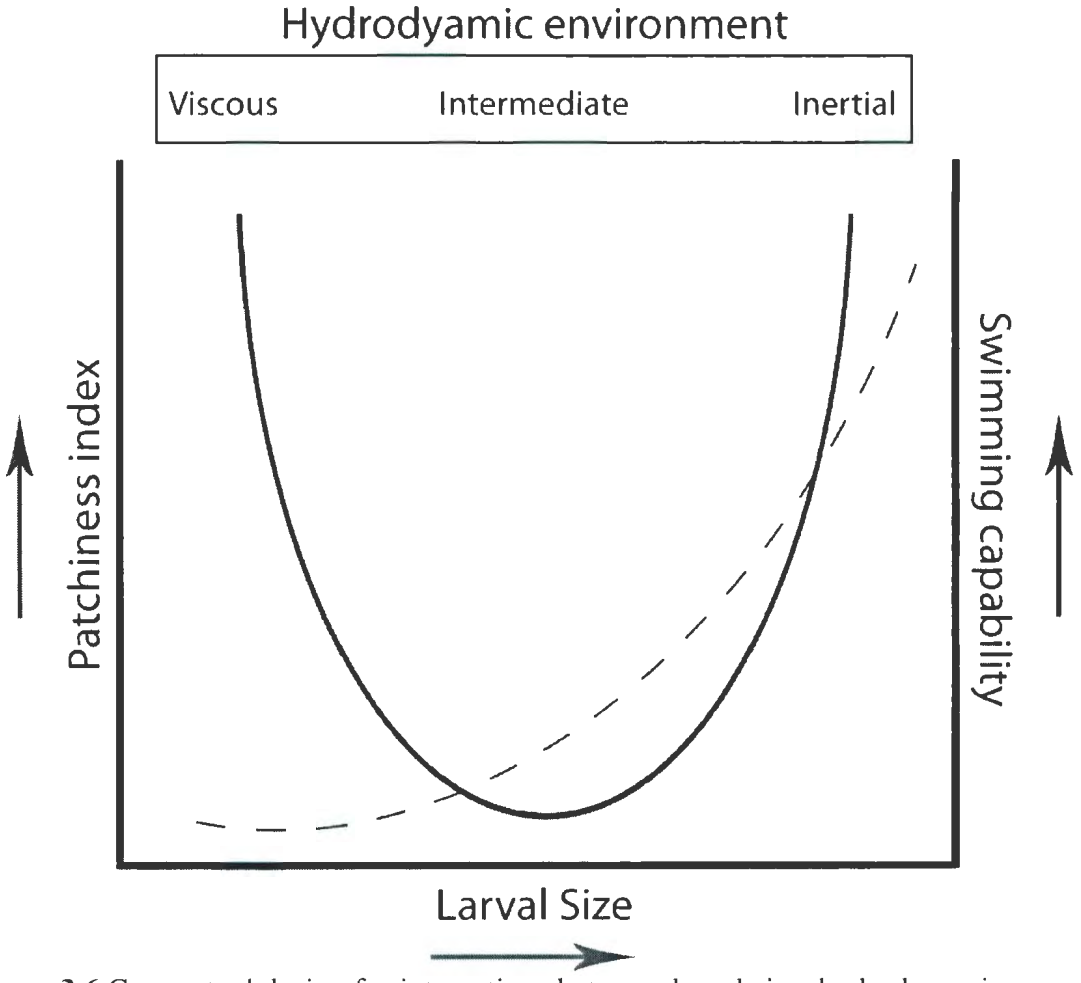


Figure 3.6 Conceptual design for interactions between larval size, hydrodynamic environment, spatial patchiness (Solid line), and swimming ability (dashed line).

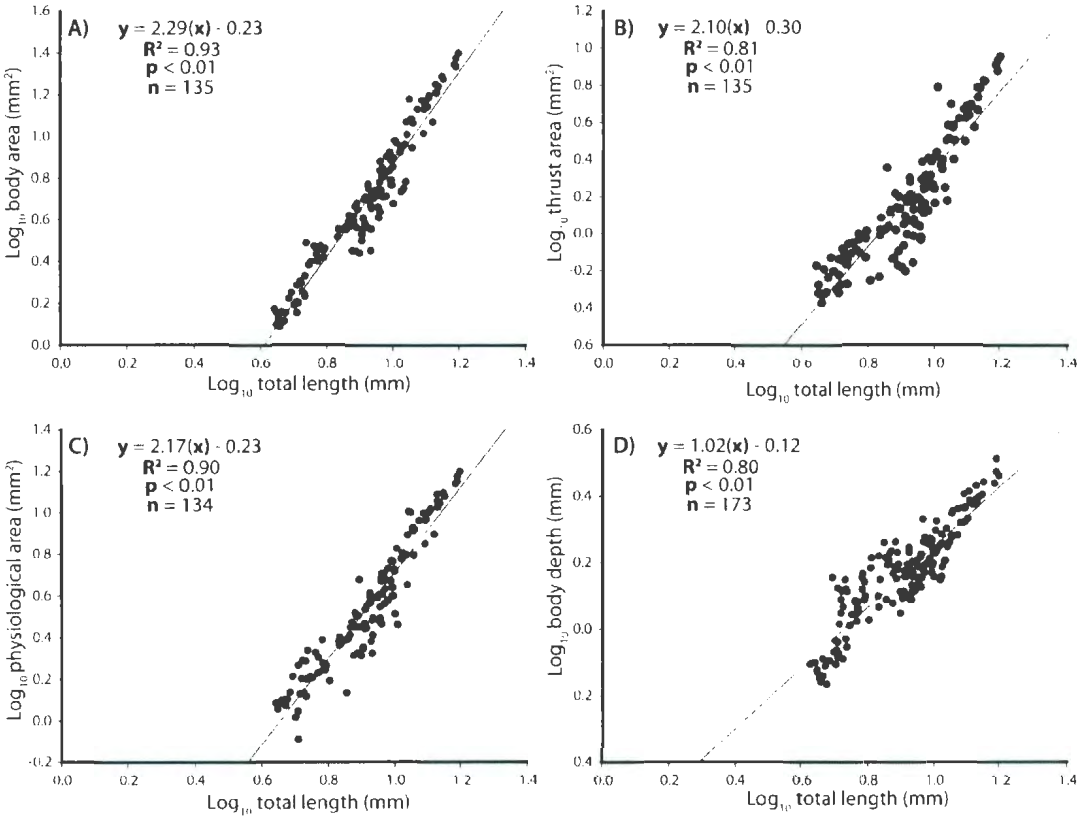


Figure 3.7 Atlantic cod (*Gadus morhua*) larvae allometric growth trajectories including reduced major axis regression results and equation. a) Body surface area positive allometric growth relative to total length b) Thrust surface area positive allometric growth relative to total length c) Physiological surface area isometric growth relative to total length d) Body depth isometric growth relative to total length. The larval image database was obtained from Lu Guan (Guan et al. 2008).

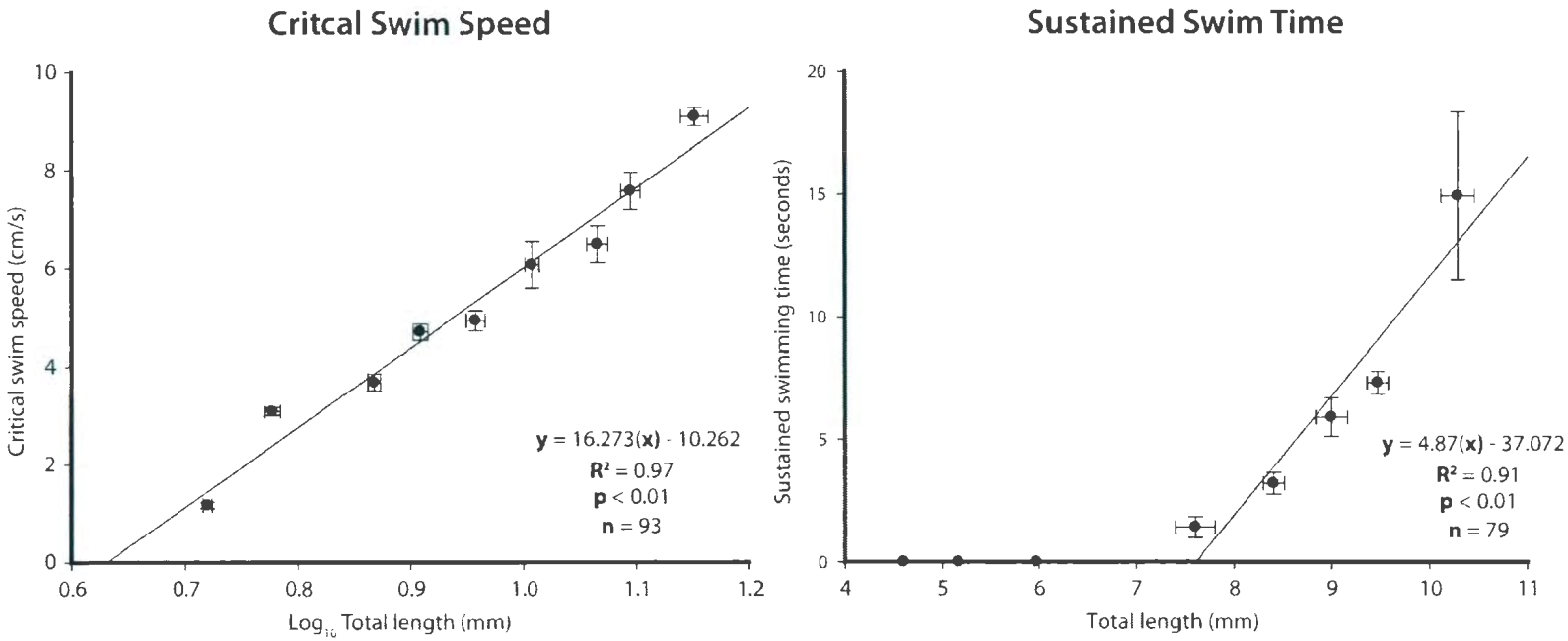


Figure 3.8 Atlantic cod (*Gadus morhua*) total length vs. kinematic performance parameters presented as weekly means starting 3 days post hatch. Data were collapsed into weekly means (± 1 standard error) represented as DAH. Plots include ordinary least squared regression analyses where y = swimming parameter and x = Total length. Sustained swimming trials were performed under 10 cm/s flow conditions. Larval image database was obtained from Lu Guan (Guan et al. 2008).

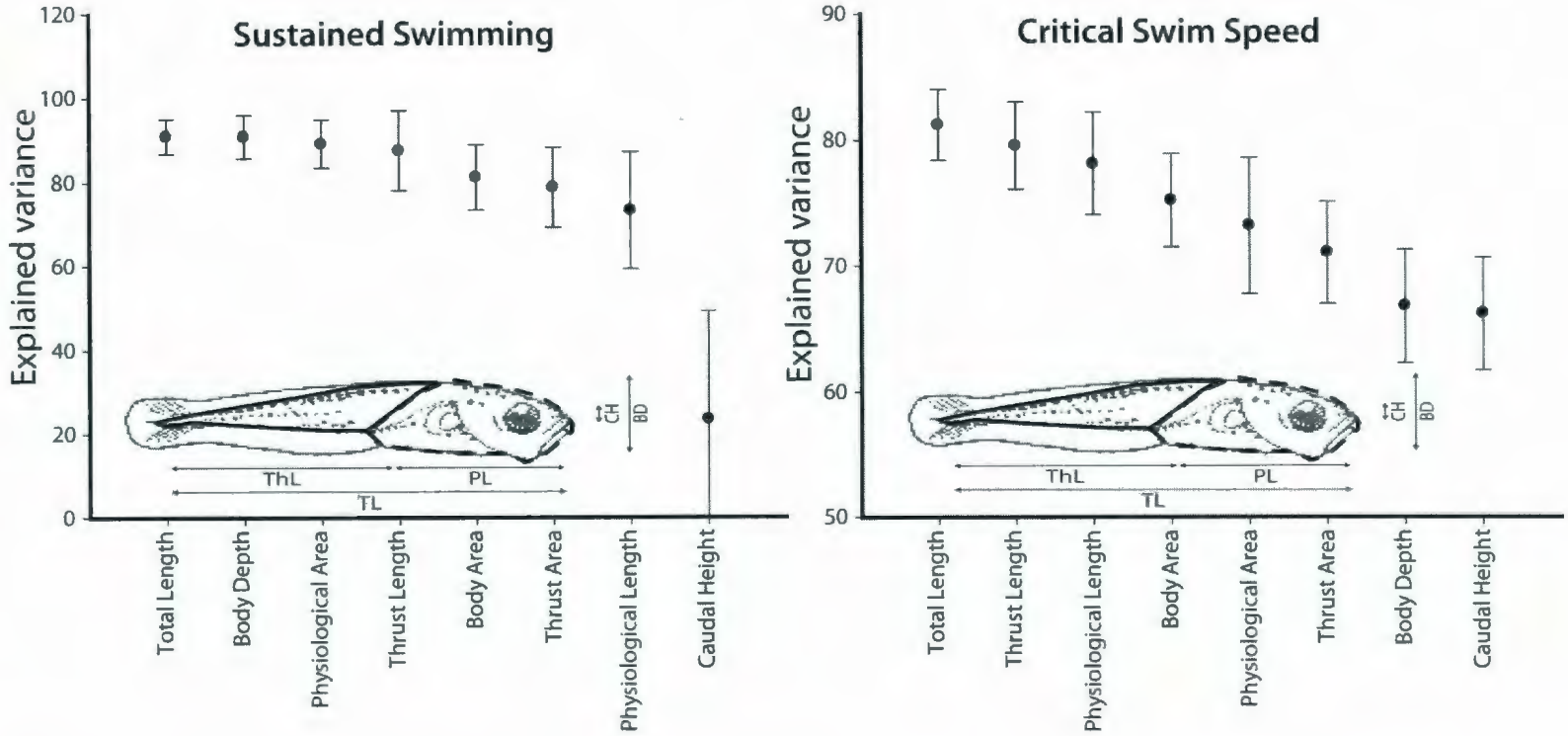


Figure 3.9 Explained variance between morphometric parameters (x axis) and swimming performance parameters for Atlantic cod (*Gadus morhua*) A – Sustained swimming speed B – Critical swim speed. Data is plotted as calculated $R^2 \pm 1$ standard deviation. Standard deviations were estimated from 1000 bootstrapped randomizations.

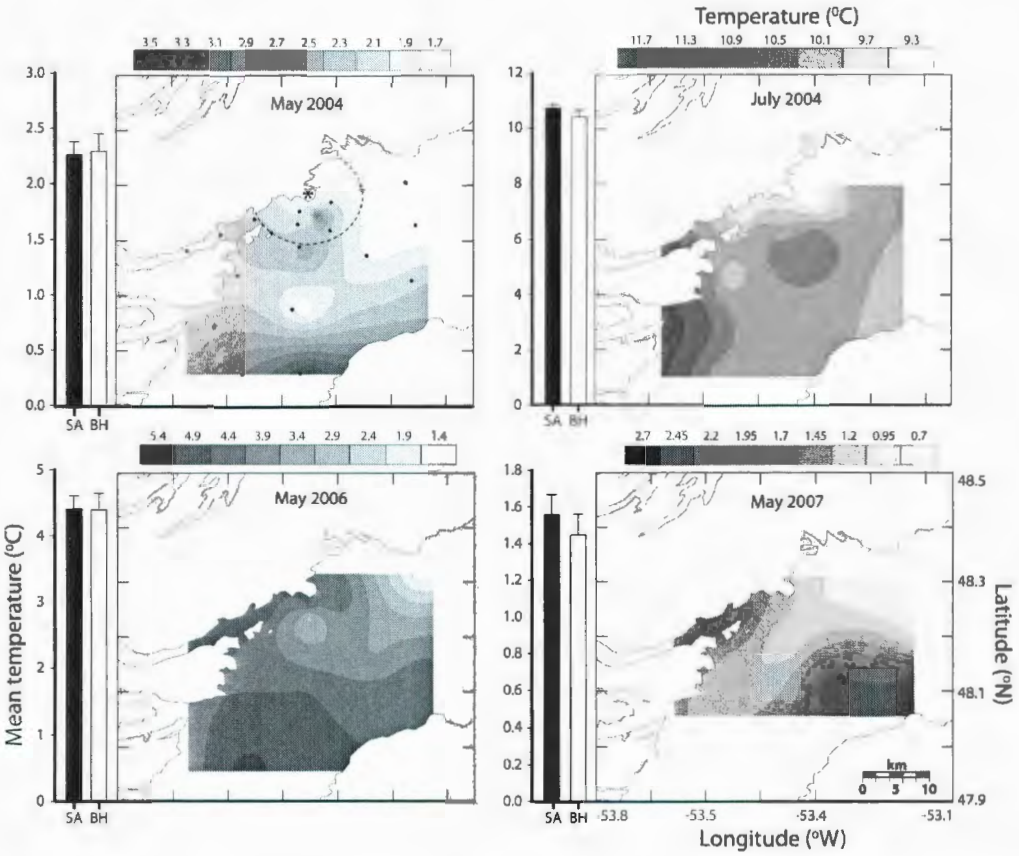


Figure 3.10 Spatially contoured CTD cast temperature data for the surface layer (average up to 5 m depth) collected during ichthyoplankton surveys of Trinity Bay 2004-2007. Bar plots represent mean temperatures ± standard error for the survey average (SA, black bar) and data from within 7 km of Bonaventure head (BH, white bar). Dashed line represents the radius of data sampled for Bonaventure Head (*) temperature calculations and dots represent station array used for all surveys.

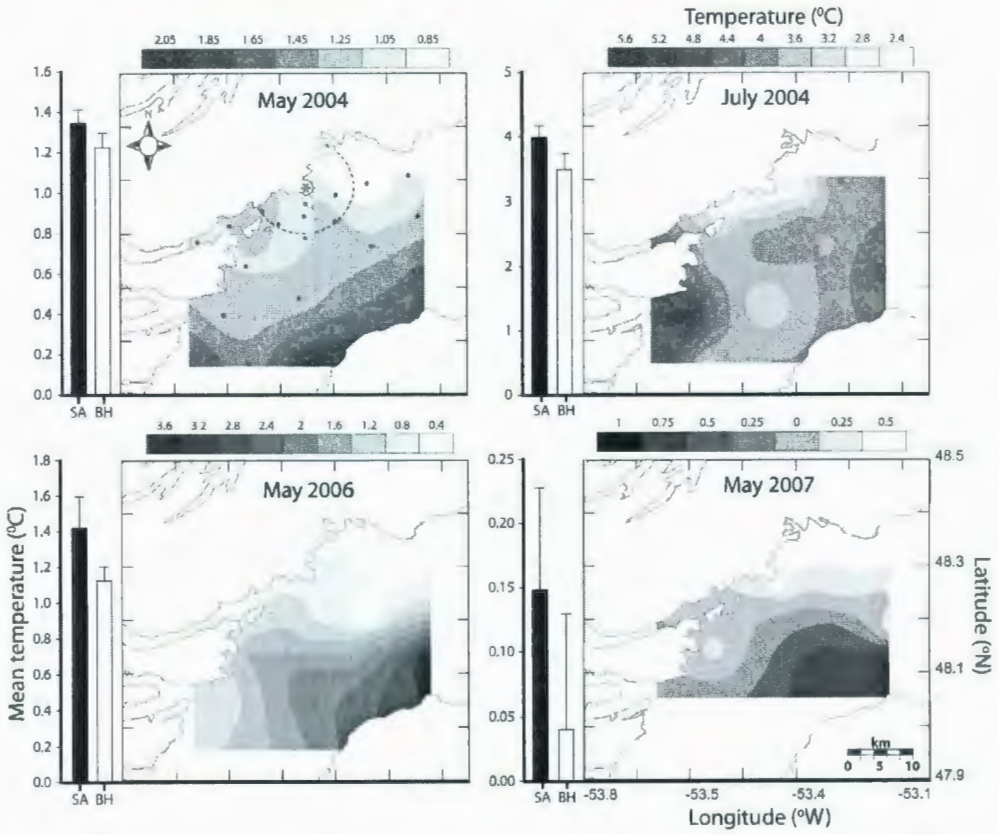


Figure 3.11 Spatially contoured CTD cast temperature data for the mixed layer (average up to 40 m depth) collected during ichthyoplankton surveys of Trinity Bay 2004-2007. . Bar plots represent mean temperatures ± ± standard error for the survey average (SA, black bar) and data from within 7 km of Bonaventure head (BH, white bar). Dashed line represents the radius of data sampled for Bonaventure Head (*) temperature calculations and dots represent station array used for all surveys.

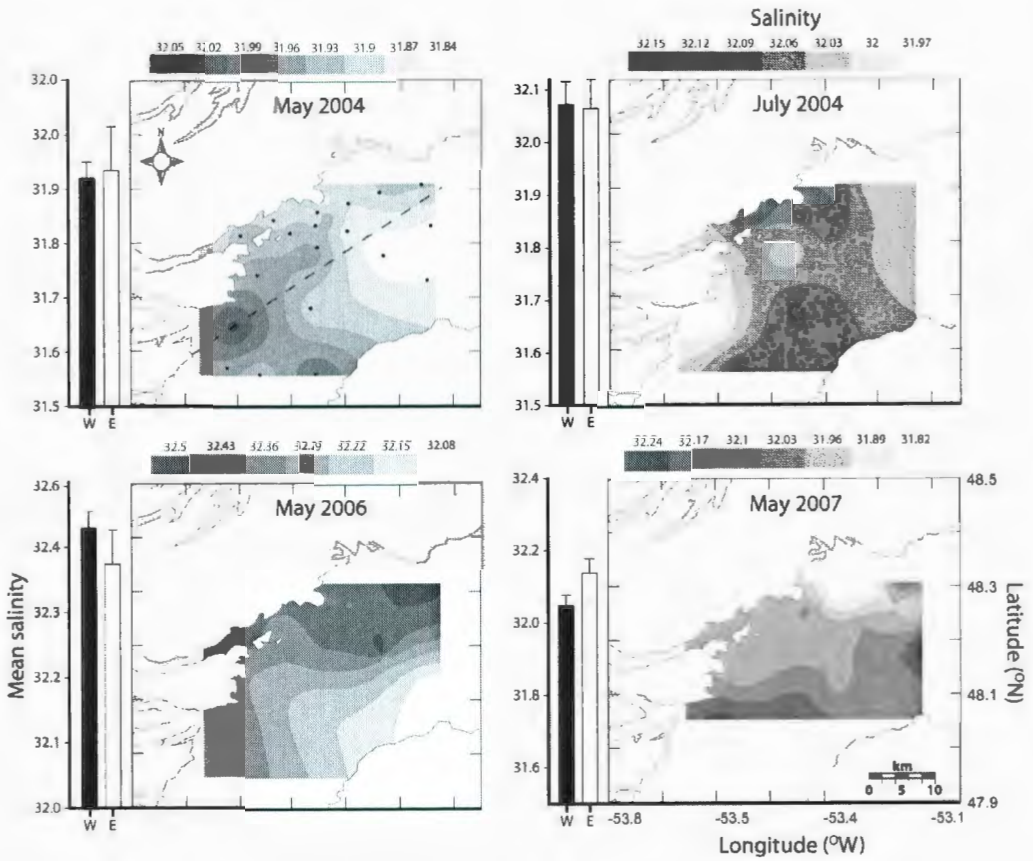


Figure 3.12 Spatially contoured CTD cast salinity data for the mixed layer (average up to 40 m depth) collected during ichthyoplankton surveys of Trinity Bay 2004-2007. Bar plots represent mean fluorescence ± 1 standard deviation for western (W, black bar) and eastern (E, white bar) Trinity Bay. Note that dashed black line denotes boundary between western and eastern Trinity Bay divisions and dots represent sample stations.

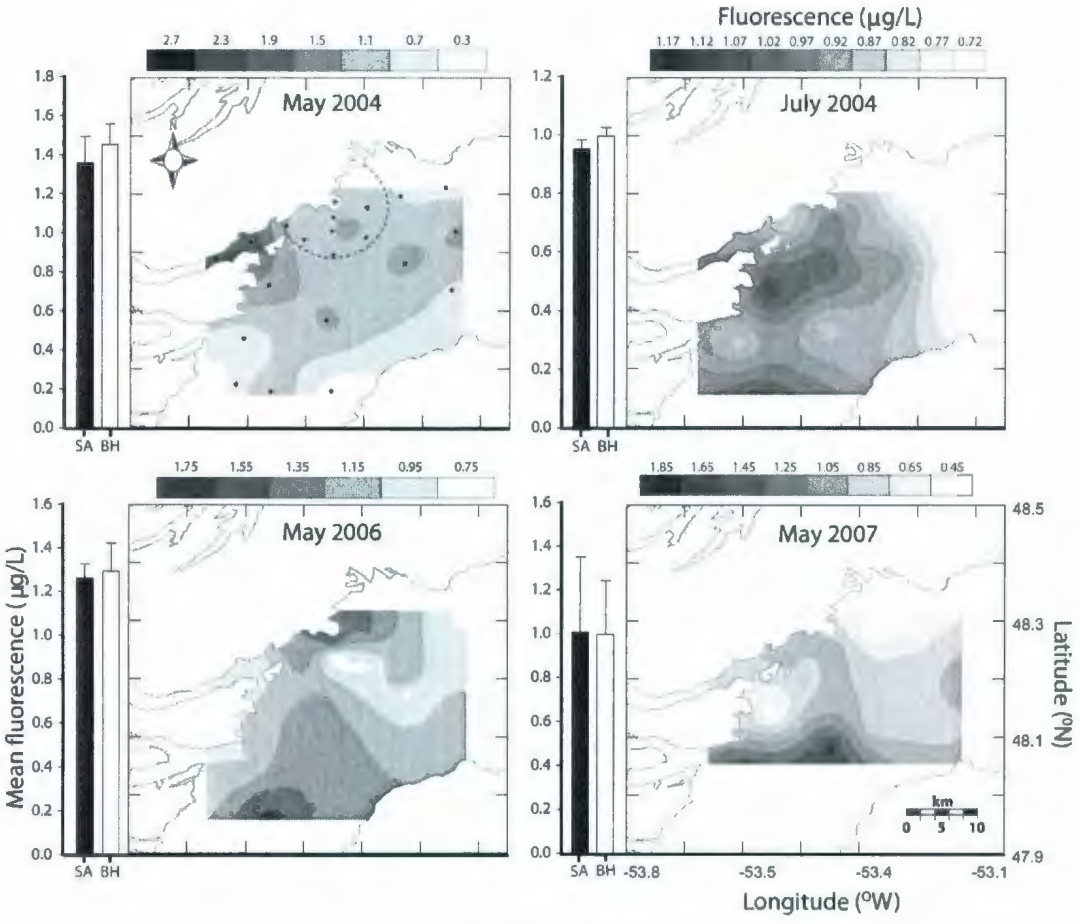


Figure 3.13 Spatially contoured CTD cast fluorescence data for the mixed layer (average up to 40 m depth) collected during ichthyoplankton surveys of Trinity Bay 2004-2007. Bar plots represent mean fluorescence ± ± standard error for western (W, black bar) and eastern (E, white bar) Trinity Bay. Note that dashed black line denotes boundary between western and eastern Trinity Bay divisions and dots represent sample stations.

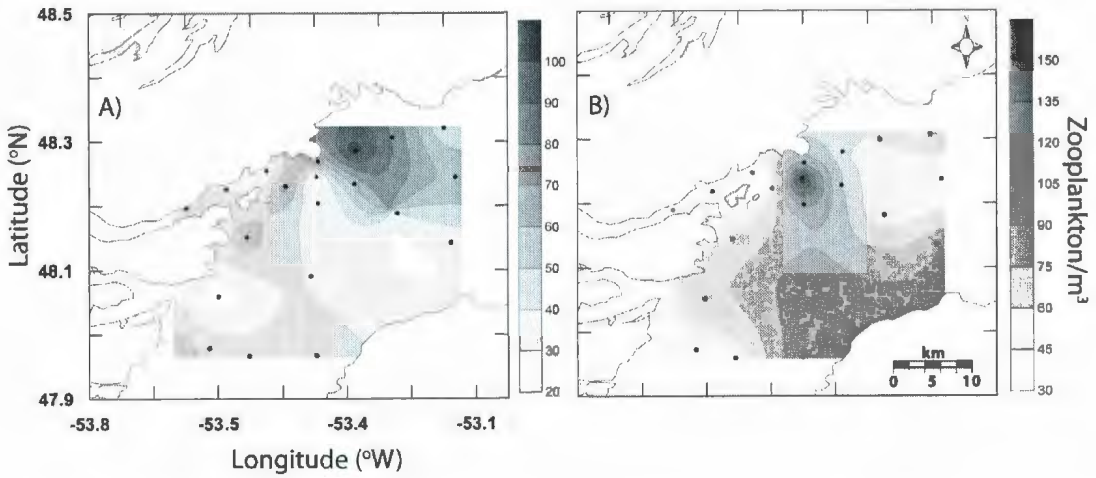


Figure 3.14 Spatially contoured zooplankton abundance (individuals per m^3) collected during May 24-26 (*A*) and May 29-31 (*B*) 2006 plankton surveys. Dots denote actual sampling locations.

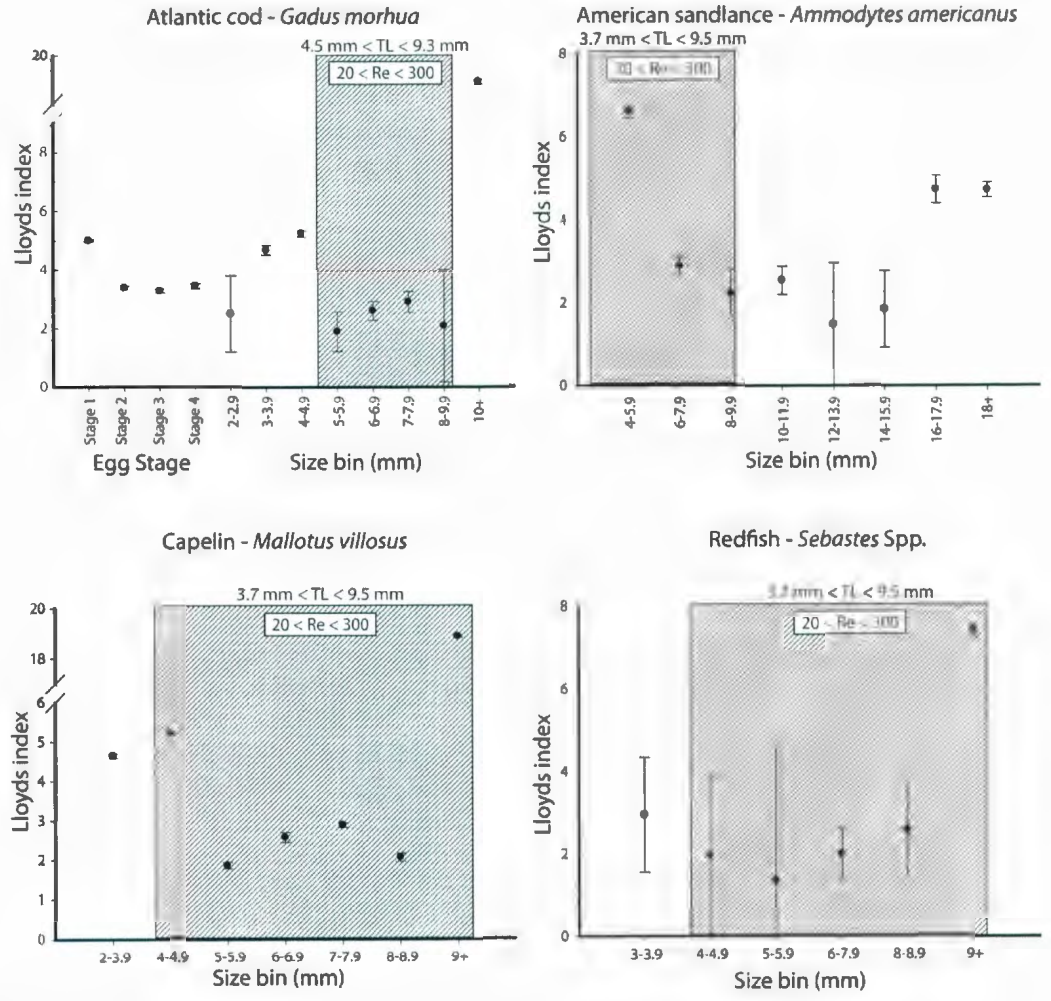


Figure 3.15 Spatial patchiness of larvae presented as Lloyd's index of patchiness ± 1 standard error. Shaded boxes represent transition zone between viscous and inertial environments. Larval data is pooled from all ichthyoplankton surveys due to constraints on catch numbers and Lloyd's index calculation.

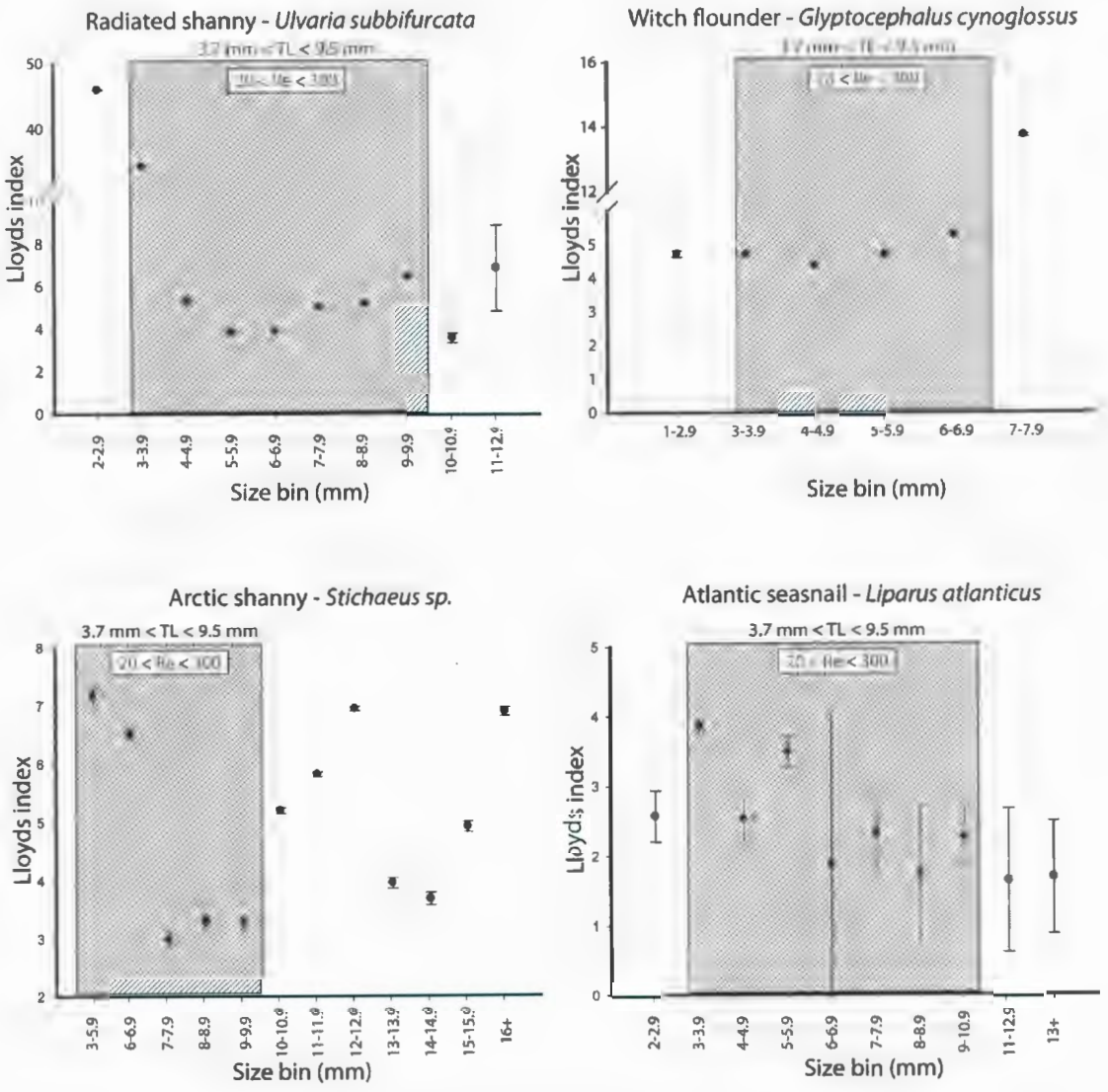


Figure 3.16 Spatial patchiness of larvae presented as Lloyd's index of patchiness ± 1 standard error. Shaded boxes represent transition zone between viscous and inertial environments. Larval data is pooled from all ichthyoplankton surveys due to constraints on catch numbers and Lloyd's index calculation.

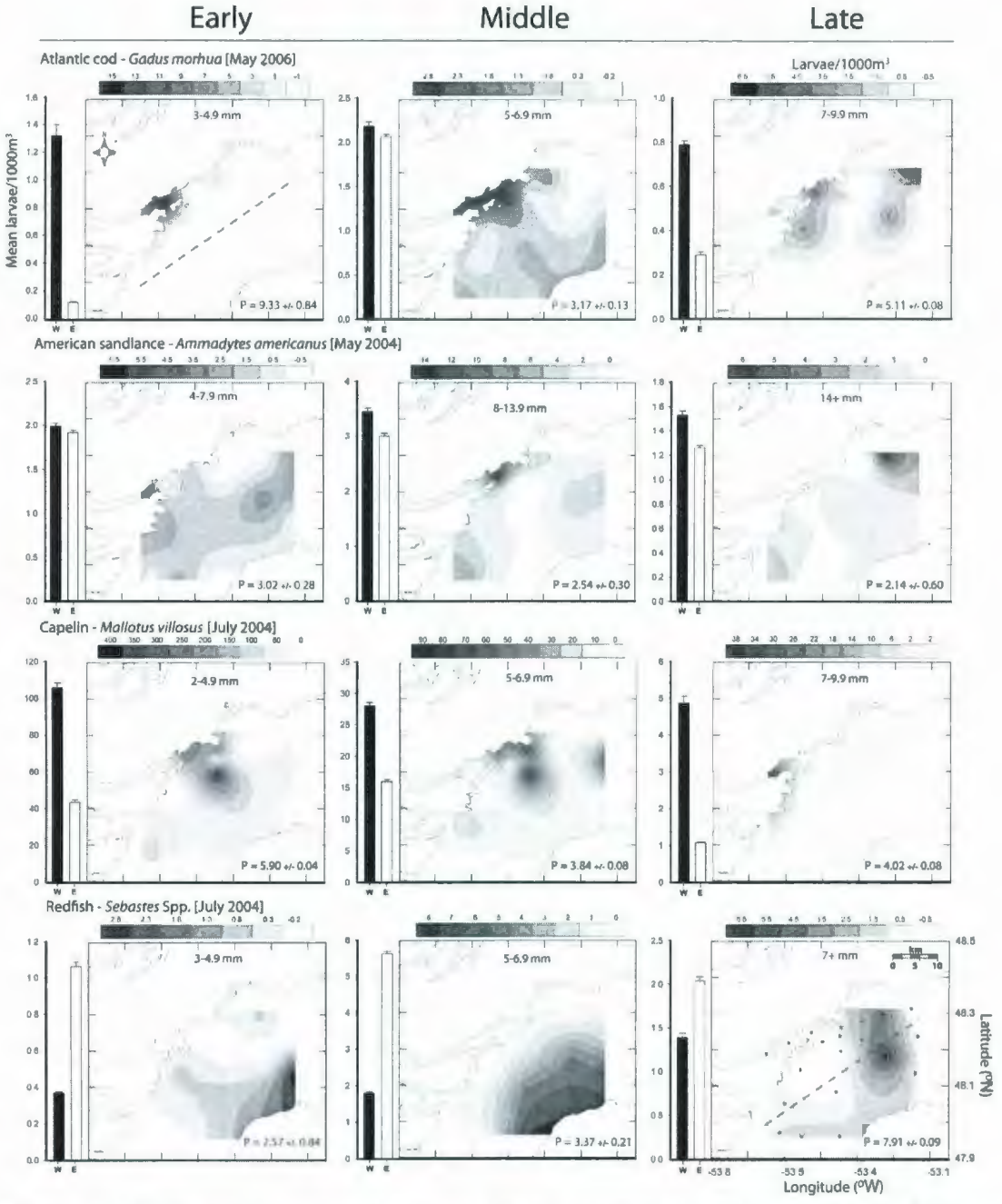
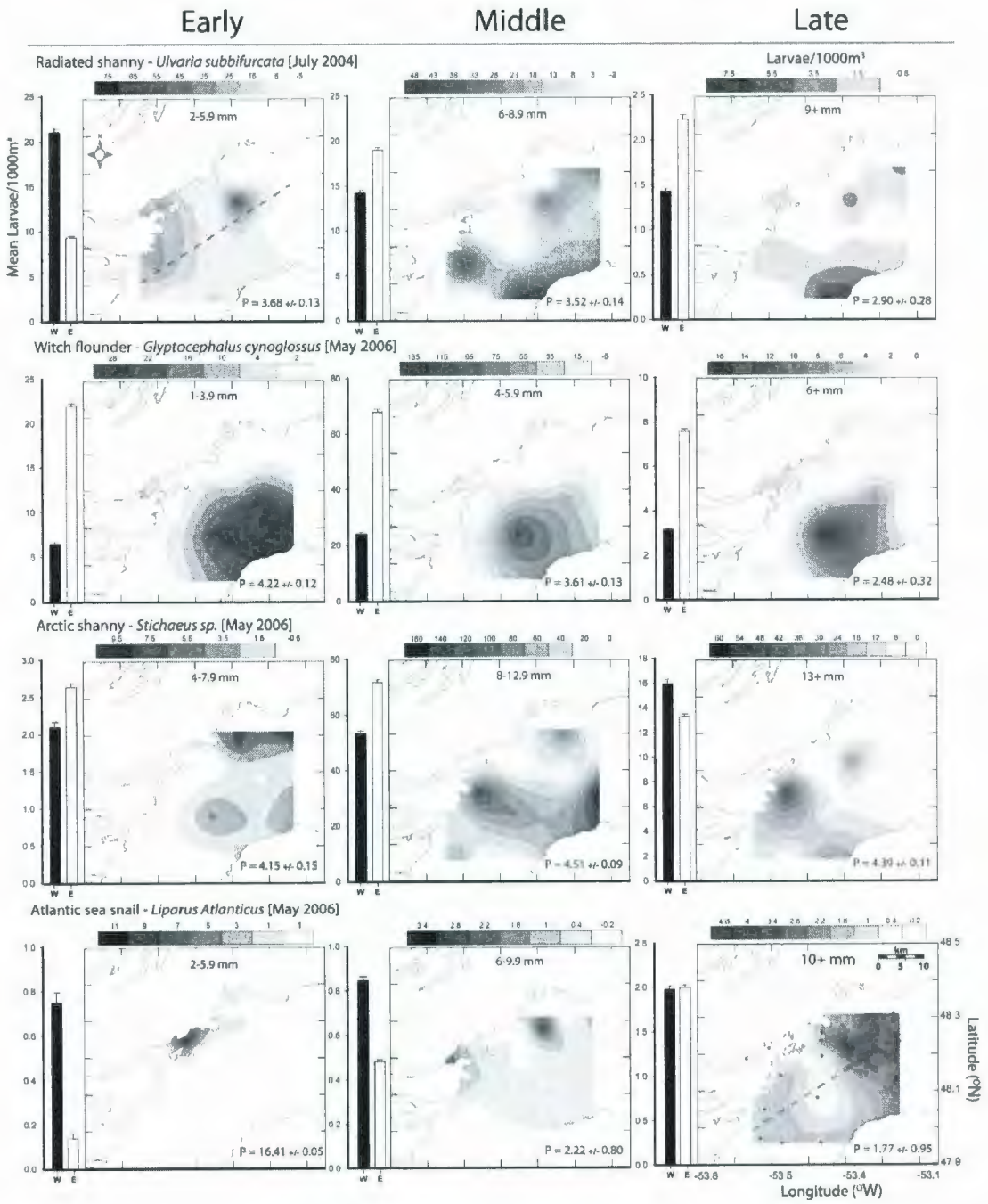


Figure 3.17 Spatially contoured species size abundance binned into early, middle and late larval development sizes. Side bars represent mean larval abundance for western (W, black bar) and eastern (E, white bar) regions of Trinity bay. Dashed line represents the boundary between the sample regions and dots represent sample stations.



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Summary and Conclusions

The literature review presented in Chapter 1 illustrates the importance of understanding linkages when developing conservation and management strategies for spatially distributed populations. Metapopulation biology, in conjunction with management and conservation efforts, offers a powerful tool that utilizes these linkages to maintain not only population number but population function (Fogarty and Botsford 2007). The linkages that maintain population connectivity and structure are often particularly important during the early life history of marine organisms where dispersal and recruitment processes define settlement areas over broad geographic areas (Harden-Jones 1968; Cowen et al. 2000). Chapter 1 illustrates the interactions between the physical environment and dispersal processes. The tandem assessment of both physical and biological data is needed to gain a comprehensive understanding of the factors that define connectivity and the maintenance of spatial structure.

The potential role of the Newfoundland inshore environment in any recovery of depleted offshore cod stocks is of great interest to scientists and managers alike. Smith Sound has the largest recorded spawning aggregation in the 2J 3KL cod stock complex and has persisted in Smith Sound for over 15 years. Dispersal estimates suggest that the Smith Sound, Trinity Bay system is highly retentive. The presence of late stage eggs and larvae in the Sound suggests residency could exceed 30 days. Larvae and eggs of all stages are strongly associated with the west coast of Trinity Bay near the mouth of Smith Sound. This spatial association does not appear to change fundamentally even during periods

when temperatures are colder, which typically leads to longer passive residency times. Though available data was limited, several lines of evidence point to the presence of oceanographic features that might contribute to the retention observed to the west coast. A spatially-consistent upwelling feature near the mouth of Smith Sound was observed in all years of the study and in previous years by other authors. Flow modelling from previous years indicated a consistent gyre feature near this coastal upwelling (Yao 1986; Tittensor et al. 2001; 2002) and proposed as a mechanism for within-bay scale retention of other species of larval fish (Dalley et al. 2002). These two features combined with the majority of spawning coinciding with warmer temperatures might play a significant role in sustaining the Smith Sound aggregation. Overall contributions to the larger 2J 3KL cod stock complex from Smith Sound might be limited and connective processes likely operate on bay sized spatial scales.

Dispersal during the early life history is both passive and active. Traditionally the capacity to evaluate the active component was limited by logistics and the view that larvae were too small and not behaviourally capable of influencing dispersal to any measurable degree (e.g., Miller et al. 1998; Fisher et al. 2000). Spatial analysis of several species of larval fishes suggests changes in spatial pattern throughout ontogeny that do not fit passive flow conditions. Increases in spatial patchiness later in ontogeny were concomitant with the transition to an inertial flow environment. These aggregations were also associated with areas where food conditions were favourable. Through these lines of evidence, I propose that active swimming behaviour significantly impacts spatial pattern and therefore dispersal. The point at which this contribution begins likely depends on the

fluid environment around the organism which defines the point of transition to the inertial flow environment.

The role of the physical environment in structuring biological processes cannot be ignored. For the Smith Sound spawning aggregation, a combination of local circulation features and timing of spawning creates a highly retentive system, which limits dispersal outside of Trinity Bay. Temperature and coastal upwelling contribute to favourable areas in terms of food conditions, which likely play a large role in the spatial pattern of larvae and subsequent recruitment patterns. Overall these results highlight how local physical features might have broad-scale biological consequences. From a management perspective, understanding the spatial structure of a population will best be achieved through a comprehensive study of local physical features and their role in defining connectivity among spatially separate sub-population units.

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